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COMPORTEMENT ALIMENTAIRE DE L'OMBLE DE FONTAINE, *SALVELINUS FONTINALIS,* ET DU SAUMON ATLANTIQUE, *SALMO SALAR*, EN MILIEU LOTIQUE.

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RÉSUMÉ

Les objectifs de cette étude étaient d'examiner les effets (1) des variations temporelles (quotidiennes et saisonnières) (2); du type d'habitat (fosse et rapide); (3) des variations d'abondance de poissons; et (4) de la disponibilité de la dérive d'invertébrés (composition taxonomique, taille et biomasse) sur les régimes alimentaires (consommation, diversité, chevauchement alimentaire et composition taxonomique) de l'omble de fontaine, *Salvelinus fontinalis*, et du saumon Atlantique, *Salmo salar*, dans des ruisseaux de l'est du Québec.

La récolte de données s'est effectuée en trois occasions au cours de l'été 1995: 23-28 juin, 17-27 juillet, 14-19 août. Nous avons échantillonné les poissons à plusieurs intervalles au cours de la journée dans des sections de ruisseaux fermées à l'aide de seines modifiées. Les poissons capturés étaient pesés, mesurés et vidés de leur contenu stomacal à l'aide d'un lavage gastrique. Parallèllement à la récolte de poissons, nous avons échantillonné la dérive à l'aide de filets à plancton disposés à l'aval de chacune des sections.

Dans un premier temps, nous avons examiné le taux de consommation des ombles de fontaine en relation avec les variations saisonnières (juin, juillet et août), le type d'habitat (fosse ou rapide), les densités d'ombles et de saumons et l'abondance des individus dans la dérive. L'omble de fontaine avait un taux maximum de consommation (mg sec de proies par g humide de poisson) en début d'après-midi (13:00) et un faible taux de consommation la nuit (1:00), alors que la biomasse de dérive (mg sec de dérive m^{-2} s^{-1}) était 7,5 fois plus élevée durant la nuit (1:00) que durant le jour (13:00). Le taux de consommation journalier

de l'omble de fontaine a décliné de 41% de juin à août. Même si la biomasse moyenne de dérive au cours de la journée n'a pas décliné de juin à août, la masse moyenne des individus dans la dérive a chuté significativement durant la saison estivale. Ainsi, le déclin saisonnier du taux de consommation des ombles aurait pu être causé par une réduction de l'abondance d'insectes de tailles profitables aux ombles. Bien que nous ayons trouvé que le taux de consommation journalier de l'omble était similaire entre les fosses et les rapides, la biomasse totale d'ombles dans les fosses était 2,8 à 6,4 fois plus élevée que dans les rapides, ce qui suggère que les fosses sont plus profitables aux ombles pour l'alimentation. Cette hypothèse est appuyée par le fait que la biomasse de dérive qui entrait dans les fosses était 2,2 fois supérieure que dans les rapides.

Dans un deuxième temps, nous avons étudié comment les variations saisonnières, le type d'habitat et les densités d'ombles et de saumons ont influencé la diversité, le chevauchement et la composition taxonomique des régimes alimentaires de l'omble de fontaine et du saumon Atlantique. Une analyse des correspondances a démontré que l'omble de fontaine consomme plus de proies terrestres et moins de proies aquatiques que le saumon Atlantique. Le saumon Atlantique a un régime alimentaire moins diversifiée dans les rapides que dans les fosses. La diversité alimentaire de l'omble de fontaine a déclinée au mois d'août comparativement à juin et juillet. Cette chute de diversité alimentaire s'est réalisée en même temps que le déclin du chevauchement alimentaire entre les deux espèces. Une analyse canonique des correspondances a révélé que la saison et les densités de compétiteurs hétérospécifiques ont affecté la composition alimentaire de l'omble de fontaine et du saumon Atlantique; la composition alimentaire du saumon différait aussi entre les fosses et les

rapides. Finalement, nous avons examiné si la consommation de la proie la plus abondante dans les estomacs d'ombles et de saumons variait en fonction des différents facteurs. La consommation d'adultes de diptères par l'omble de fontaine était influencée par une interaction entre la saison et les densités de saumons, alors que la consommation de larves d'éphéméroptères par le saumon Atlantique était influencée par les densités d'ombles de fontaine. Ces résultats démontrent qu'il peut s'avérer nécessaire de prendre en compte les variations saisonnières, le type d'habitat et les densités de poissons, ainsi que les interactions entre ces facteurs, lorsqu'on étudie le comportement alimentaire des poissons.

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AVANT-PROPOS

Le mémoire qui suit est écrit sous forme de deux articles scientifiques en version anglaise. Les auteurs sont, pour le premier article (Chapitre I), Alain Guitard et Marco A. Rodríguez. Pour le deuxième article (Chapitre II), les auteurs sont Alain Guitard, Marco A. Rodríguez et Simon Trépanier, ce dernier pour son implication dans la caractérisation des ruisseaux et de la densité des populations de poissons. Le journal visé pour les deux articles est le Journal Canadien des Pêches et des Sciences Halieutiques.

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Figure 8. Percent consumption (numbers) of ephemeropteran larvae by Atlantic salmon in pools (filled) and riffles (empty) in relation to charr density and sampling period (June: squares; July: triangles; August: circles). Least-square regression lines are shown also.

INTRODUCTION

Problématique

La sélection naturelle favoriserait les individus dont les caractéristiques comportementales, physiologiques et morphologiques permettent d'obtenir le succès reproducteur le plus élevé (Krebs et McCleery 1984). Ces caractéristiques peuvent être reliées à la distribution spatiale des animaux, et par conséquent à la sélection de l'habitat (Abrahams 1986). Il est d'ailleurs reconnu que les stratégies comportementales de quête alimentaire jouent un rôle important dans la distribution spatiale des animaux (Krebs et al. 1978; Kacelnik et al. 1992).

Les différents modes d'utilisation de l'habitat, la structure de la communauté et l'intensité des interactions entre les compétiteurs potentiels peuvent être influencés par la qualité des différents types d'habitats (Pimm et al. 1985; Silvertown et Wilson 1994). La profitabilité reliée à un habitat peut dépendre, entre autres, des variations saisonnières (Morris 1996), de la qualité et quantité de la nourriture disponible (Abrams 1991) et des interactions avec des compétiteurs conspécifiques ou hétérospécifiques (Pimm et al. 1985; Milinsky et Parker 1991). En conséquence, ces facteurs peuvent influencer les aspects reliés à la consommation des animaux (composition taxonomique des proies, quantité et contenu énergétique de la nourriture consommée) (Persson 1986; Diehl 1993), et donc à leur budget énergétique (Jobling 1994).

Les ruisseaux des régions tempérées permettent d'étudier les effets de l'habitat, des

variations saisonnières, de la disponibilité de la nourriture et des compétiteurs potentiels sur l'alimentation des poissons. La plupart de ces ruisseaux sont caractérisés par une alternance de fosses et de rapides, des habitats qui diffèrent en fonction de la vitesse du courant, de la profondeur de la colonne d'eau, ainsi que du type de substrat (Gibson et al. 1993). De plus, les ressources alimentaires disponibles dans la dérive, principalement des invertébrés qui dérivent dans la colonne d'eau, varient généralement en nombre et en biomasse pendant la journée (Waters 1972) et durant la saison estivale (Angermeier 1982). Par ailleurs, l'occupation de deux ou plusieurs espèces de salmonidés est fréquente. Ces salmonidés partagent souvent les mêmes ressources alimentaires de par leurs ressemblances morphologiques, physiologiques et comportementales (Power 1980; Hearn 1987). Les salmonidés peuvent compétitionner pour la nourriture disponible ou l'habitat avec des individus de la même espèce ou d'une autre espèce (Hearn 1987).

La consommation de proies par les salmonidés a été utilisée comme mesure de la profitabilité d'un habitat puisque les salmonidés semblent se distribuer de façon à maximiser l'efficacité de la quête alimentaire (Fausch 1984; Puckett et Dill 1985). Peu d'études ont été réalisées dans le but de comparer la production nette de nourriture dans les fosses et les rapides par rapport à l'alimentation des salmonidés. Cependant, des études ont démontré que les nymphes d'éphéméroptères ainsi que les larves de trichoptères, de simuliidés et de chironomides, différaient en nombre dans les fosses et les rapides (Egglishaw 1967; Allan 1995). Des différences physiques notables pourraient occasionner des différences de productivité de nourriture entre ces deux habitats. Les fosses retiendraient plus de proies par

précipitation de la colonne d'eau vers le substrat, comparativement aux rapides où le courant est trop fort pour favoriser le dépôt des proies (McLay 1970).

L'omble de fontaine, *Salvelinus fontinalis*, et le saumon Atlantique, *Salmo salar*, vivent en sympatrie dans plusieurs ruisseaux de l'Est du Canada. Ces deux salmonidés consomment principalement de la dérive (McNicol et al. 1985). Il a été suggéré que l'omble et le saumon sont des prédateurs diurnes, et que la consommation de proies par l'omble aurait tendance à baisser à mesure que la saison estivale progresse (Gibson et al. 1984). Lorsqu'ils sont en allopatrie (présence d'une seule espèce), ces salmonidés utilisent aussi bien les fosses que les rapides, alors qu'en sympatrie (présence de l'omble et du saumon), l'omble de fontaine est plus abondant dans les fosses et moins nombreux que le saumon Atlantique dans les rapides, surtout tard dans la saison estivale lorsque la disponibilité de nourriture est réduite (Gibson 1973, Gibson et al. 1993). Il semblerait que des interactions compétitives par exploitation et par interférence favorisant le saumon seraient en cause (Gibson et al. 1993; Rodríguez 1995).

Le saumon Atlantique et l'omble de fontaine ont des différences morphologiques notables. Le saumon possède une densité corporelle plus grande et des nageoires pectorales proportionnellement plus larges que l'omble, ce qui lui permet de se poser plus efficacement sur le substrat comparativement à l'omble, qui doit utiliser une position plus élevée au-dessus du substrat (Gibson 1973; Gibson et al. 1993). Ces différences pourraient être reliées aux stratégies divergentes du comportement alimentaire entre le saumon et l'omble lorsque la compétition entre les deux espèces devient importante. Le saumon, naturellement plus

agressif, créerait des territoires occasionnels lorsque la nourriture devient réduite, ce qui pourrait pousser l'omble à changer son comportement, d'une alimentation stationnaire principalement axée sur de la dérive, à une alimentation active à la surface de la colonne d'eau (Thonney et Gibson 1989). Il se pourrait donc que les différences morphologiques entre les deux espèces permettent à l'omble d'adopter une stratégie alternative pour s'alimenter, afin de palier à une hausse de la compétition par le saumon.

Peu d'études ont porté sur la façon dont la consommation de proies par les salmonidés diffère dans les fosses et les rapides (Bridcut et Giller 1993), ou sur l'effet des densités de ces deux espèces sur la consommation individuelle (Forrester et al. 1994). Certains modèles théoriques prédisent que la profitabilité individuelle est la même entre deux ou plusieurs habitats lorsque la distribution des individus est libre entre ces habitats ('ideal-free distribution'; Fretwell et Lucas 1970). Si, par contre, des individus de la même espèce ou d'une espèce compétitrice empêchent le libre accès aux ressources (nourriture, espace) à d'autres individus, la profitabilité individuelle pourrait être différente entre ces habitats (Fretwell 1972).

Les objectifs de cette étude étaient d'examiner les effets (1) des variations temporelles (quotidiennes et saisonnières) (2); du type d'habitat (fosse et rapide); (3) des variations d'abondance de saumons et d'ombles; et (4) de la disponibilité de la dérive d'invertébrés (composition taxonomique, taille et biomasse) sur les régimes alimentaires (consommation, diversité, chevauchement alimentaire et composition taxonomique) de l'omble de fontaine et du saumon Atlantique dans des ruisseaux de l'est du Québec.

Échantillonnage sur le terrain

Les travaux ont eu lieu sur deux ruisseaux de deuxième et troisième ordres dans la Vallée de la Matapédia en Gaspésie (Québec): le ruisseau Chandler, situé dans la Réserve faunique de Matane et le ruisseau Gunn, situé dans la Zone d'Exploitation Contrôlée Casault (ZEC Casault).

Dans le ruisseau Chandler, on retrouve une abondance relativement élevée de saumons et d'ombles ainsi qu'une faible quantité de naseux des rapides (*Rhinichthys cataractae*) et de chabots visqueux (*Cottus cognatus*). Le ruisseau Gunn possède deux communautés ichtyennes distinctes séparées par un obstacle infranchissable. Dans la partie nord (Gunn Nord), on retrouve de l'omble de fontaine et une quantité moindre de saumons, alors que dans la partie sud (Gunn Sud), le saumon et l'omble vivent en proportions relativement semblables. La pêche était interdite dans tous les ruisseaux mentionnés au cours des années 1994 et 1995.

L'échantillonnage sur le terrain s'est déroulé en 1994, et à trois occasions durant la période estivale de 1995: du 23 au 30 juin, du 17 au 27 juillet et du 14 au 19 août. Les ombles et saumons étaient récoltés à la pêche électrique (modèle Smith-Root 15-C) dans des sections individuelles de ruisseaux (fosses et rapides) fermées à l'aide d'un filet modifié (mailles de 6 mm). Deux sections d'une combinaison fosse-rapide étaient échantillonnées simultanément à chaque journée. Les heures de récolte des poissons étaient 3h00, 7h00, 11h00, 15h00, 19h00 et 23h00.

Les poissons récoltés ont été anesthésiés au MS-222, mesurés à la longueur à la

fourche (1 mm), pesés (0,01 g) et immédiatement évacués de leurs contenus stomacaux afin d'éviter une prolongation de l'évacuation gastrique. Les contenus stomacaux ont été préservés individuellement dans des bouteilles de 120 ml avec de l'isopropanol 60%. Le lavage gastrique, une méthode non-léthale et efficace (Light et al. 1983), a été utilisé pour évacuer le contenu stomacal des poissons. Un manipulateur introduisait un tube provenant d'une seringue hypodermique de grosseur variable dans l'estomac du poisson et provoquait une entrée d'eau à l'aide d'une pompe remplie d'eau. La manipulation d'un poisson dépassait rarement une minute et le poisson était désinfecté au bleu de méthylène avant d'être remis à l'eau. Nous avons sacrifié 57 ombles de fontaine et 31 saumons Atlantique pour vérifier l'efficacité du lavage gastrique. Au total, 98,8% du nombre de proies contenues dans l'estomac d'ombles et 99,5% du nombre de proies retrouvées dans les estomacs de saumons ont été évacuées à l'aide de la méthode.

Parallèlement à la récolte de poissons, nous avons échantillonné la dérive durant les mêmes intervalles de temps. Un filet à plancton (30 cm largeur x 46 cm longueur, mailles de 250 μm) a été disposé à l'amont de chaque section, et le contenu du filet fût récolté tout juste avant la pêche électrique et conservé dans du formol 20%. Une fois la session de pêche électrique terminée, les filets étaient remis à l'eau pour le prochain échantillonnage.

Nous avons également estimé les densités de poissons environ une à deux semaines avant l'échantillonnage de poissons et de dérive. Dans les mêmes sections, des poissons ont été capturés par pêche électrique selon la méthode du retrait successif en milieu fermé (Rexstead et Burnham 1991). Un minimum de trois passages successifs ont été utilisés pour

calculer les densités par unité de surface (m^2).

Au laboratoire, les contenus stomacaux étaient séparés des parasites, roches et des débris végétaux afin de ne pas biaiser les estimations des taux de consommation et d'évacuation. Ensuite, les proies retrouvées dans les contenus stomacaux étaient identifiées avec une loupe binoculaire (47 types de proies), et le contenu fut filtré et pesé en poids humide (0,0001 g) et en poids sec après séchage à 65 °C durant 24 h dans un four à aération. Un appareil de sous-échantillonnage volumétrique a été utilisé pour homogénéiser la dérive et y retirer entre 3 et 5 réplicats représentant environ 25 % du volume total de dérive (Wrona et al. 1982).

Consommation des ombles

Les taux de consommation instantannée et journalier ont été estimés en poids relatif (RCM; Hyslop 1980) pour tenir compte des différences de poids des poissons:

$$RCM = \frac{\text{mg poids sec des proies}}{\text{g poids humide des poissons}}$$

Le taux de consommation instantannée a été calculé pour des intervalles de 4 h selon Elliott et Persson (1978):

$$C_t = \frac{(W_f - W_o e^{-Rt})Rt}{1 - e^{-Rt}}$$

où R est le taux d'évacuation gastrique, W_0 est la moyenne géométrique de RCM au début de l'intervalle d'échantillonnage et W_f est la moyenne géométrique à la fin de l'intervalle de 4 h.

Afin d'éviter certains biais reliés au manque de fermeture journalier des intervalles d'échantillonnage ('lack of closure'), le taux de consommation journalier (C) a été calculé selon la méthode corrigée du modèle de Eggers (Hayward 1991):

$C = (W_T \cdot R \cdot T) + (W_f - W_o)$

où R est le taux d'évacuation gastrique, T est le temps entre le début et la fin de l'échantillonnage (20 h pour cette étude), W_o est la moyenne géométrique de RCM au début de l'échantillonnage, W_f est la moyenne géométrique à la fin de l'échantillonnage et W_T est la moyenne géométrique de RCM pour tous les poissons capturés durant la période d'échantillonnage de 20 h.

Afin d'estimer les taux d'évacuation des contenus stomacaux, nous avons capturé une quantité variable d'ombles (13-31 par échantillonnage) en 1994 et 1995. Les poissons étaient disposés en faibles densités dans des bacs libres de nourriture. Les contenus stomacaux de 4 à 7 ombles furent récupérés en différentes occasions sur des périodes de 20 heures. Les taux d'évacuation ont été estimés selon l'équation suivante:

$\ln W_t = b_0 + b_1 \ln W_f + R \cdot t$

où t est le temps d'inanition, W_t est le poids moyen des contenus stomacaux pour tous les poissons capturés au temps t, W_f est le poids moyen des poissons récoltés au temps t, b_0 et b_1 sont des constantes et R est le taux d'évacuation gastrique. En tout, 8 taux d'évacuation ont été calculés pour les fins de l'étude.

La biomasse de dérive (mg poids sec m^{-2} s^{-1}) et l'abondance de dérive (nombre m^{-2} s^{-1}) ont été calculées comme la quantité de dérive en passage sur une superficie de 1 m^2 de

colonne d'eau par seconde (Fausch 1984).

Composition alimentaire des poissons

La diversité alimentaire de l'omble de fontaine et du saumon Atlantique a été calculée pour des sections individuelles de ruisseaux avec la réciproque de l'indice de dominance de Simpson (1/D; 'Simpson's diversity'), modifiée pour un nombre déterminé de proies (Magurran 1988):

$$\frac{1}{D} = \frac{1}{\sum_i \frac{(n_i)(n_i - 1)}{(N)(N-1)}}$$

où n_i est le nombre de proies du taxon i et N est le nombre total de proies. L'indice de diversité de Simpson varie pour cette étude de 1 (seulement 1 taxon présent dans les contenus stomacaux) à 47, où tous les taxons sont représentés.

Le chevauchement alimentaire des ombles de fontaine et des saumons Atlantique a été quantifié pour des sections individuelles avec l'indice de Pianka (Pianka 1973):

$$\alpha_{j,k} = \frac{\sum_i (p_{ij} \times p_{ik})}{\sqrt{(\sum_i p_{ij}^2 \times \sum_i p_{ij}^2)}}$$

où p_{ij} et p_{ik} sont les proportions de proies de taxon i, utilisé par les espèces *j* ou *k*. L'indice de Pianka varie de 0 (aucun chevauchement) à 1 (composition alimentaire identique entre les deux espèces).

Afin d'examiner les variations de composition alimentaire entre les ombles de fontaine et les saumons Atlantique, nous avons utilisé une forme d'analyse de

correspondence ('Detrended correspondance analysis'; ter Braak 1990). Cette technique d'ordination permet de distribuer dans l'espace d'un graphique, les différentes sections où sont représentés des ombles ou des saumons. Nous pouvons ainsi analyser visuellement et de façon objective, les différences entre les deux espèces ainsi que les types de proies responsables pour les différences notées. Pour visualiser les variations de la composition alimentaire des ombles et saumons en fonction de la période de la saison, de l'habitat et des densités de poissons, l'analyse canonique de correspondance a été utilisée (CCA; ter Braak 1990). À l'aide de cette analyse, il est possible de décrire collectivement la consommation des proies en réponse aux effets de la saison, de l'habitat et des densités de poissons.

CHAPITRE I

FOOD CONSUMPTION BY STREAM-DWELLING BROOK CHARR, *SALVELINUS FONTINALIS*: TEMPORAL VARIATION AND INFLUENCE OF HABITAT TYPE AND POTENTIAL COMPETITORS.

Abstract. This study examined patterns of daily and seasonal (June, July, August) variation in food consumption of brook charr, *Salvelinus fontinalis*, and tested whether habitat type (pools, riffles), population densities of brook charr and Atlantic salmon, *Salmo salar*, and drift abundance influenced food consumption. Fish were collected in small streams of eastern Quebec by electrofishing in closed stream sections. The daily pattern of instantaneous food consumption (mg DM prey g WM $fish^{-1}$ 4 h^{-1}) was strongly unimodal with a peak near noon (13:00) and near-zero consumption at night (1:00); drift biomass was 7.5 times higher at night (1:00) than at midday (13:00). Daily food consumption (mg DM prey g WM $fish^{-1}$ day^{-1}) declined by 41 % from June to August. Even though daytime drift biomass did not decline over the summer, mean mass of individual prey in drift decreased significantly from June to August. Seasonal decline in daily food consumption may thus arise from a reduction of large, energetically-profitable prey in the drift over the summer. Neither habitat type nor population densities had an apparent effect on daily food consumption. Daytime drift biomass was 2.2 times higher in pools than in riffles. Although daily food consumption per unit fish mass was similar in the two habitats, brook charr biomass, and thus total food consumption, was 2.8 to 6.4 times higher in pools than in riffles, suggesting that food availability for brook charr is higher in pools.

Introduction

Food consumption is the prior element of energetic budgets of all fish species (Brett and Groves 1979; Jobling 1994). Because of the relevance of food consumption to individual fitness, numerous studies of habitat selection have used food consumption as a measure of habitat profitability (e.g. Krebs et al. 1978; Kacelnik et al. 1992). Habitat profitability may thus be influenced by factors affecting food consumption, such as temporal variation in food availability, physical habitat structure, and interactions with conspecific and heterospecific competitors (Pimm et al. 1985; Morris 1996).

In streams, the abundance (numbers and biomass) of drifting invertebrates, the main food source for particulate-feeding fish, shows considerable daily (Brittain and Eikeland 1988; Allan 1995) and seasonal (Angermeier 1982; Power 1993) variation. The influence of temporal variation in various biotic and abiotic factors on food consumption by stream-dwelling salmonids is well documented (temperature: Brett and Groves 1979; drift quantity: Gibson et al. 1984; light intensity: Wilzbach et al. 1986). In contrast, relatively less attention as been paid to differences in salmonid feeding between habitat types (Egglishaw 1967; Bridcut and Giller 1993), or to the effects of competitor abundances on food consumption by salmonids (Forrester et al. 1994).

Theoretical models of habitat selection predict that individual profitability should be equalized across habitats whenever animals are able to redistribute themselves freely among habitats (ideal free distribution, Fretwell and Lucas 1970; Milinsky and Parker 1991). If, however, conspecifics or heterospecifics behaviourally interfere with access to resources

(food, space, shelter), individual profitability may differ among habitats (Fretwell 1972; Sutherland 1983). The distribution of sympatric brook charr, *Salvelinus fontinalis*, and Atlantic salmon, *Salmo salar*, in pool and riffle habitats, has been analysed by means of a theoretical model of density-dependent habitat selection (Rodríguez 1995). The results of that study suggested that for both species, population densities were adjusted so as to equalize the mean profitability among habitats; brook charr favoured pools, whereas Atlantic salmon favoured riffles.

This study examines patterns of daily and seasonal variation in food consumption of stream-dwelling brook charr, and tests whether drift abundance (total biomass and mean individual mass), habitat type (pool or riffle), and population densities of brook charr and Atlantic salmon influence food consumption by brook charr. Possible implications of inter-habitat differences in food consumption and biomass of brook charr to habitat profitability are discussed.

Materials and methods

Study sites

Field work was conducted in the summer of 1995 in two separate reaches of Gunn Creek, in the Matapedia Valley, eastern Quebec, Canada. In the upstream reach (North Gunn; 48 ° 32' N; 67 ° 07' W), brook charr is found in near-allopatry (range in density: 31 - 228 ind. per 100 m^2) whereas in the downstream reach (South Gunn; 48 ° 32' N; 67 ° 06' W), brook charr (5 - 162 ind. per 100 m^2) and Atlantic salmon (1 - 130 ind. per 100 m^2) are sympatric. Stream temperature, measured in June, July, and August, ranged from 12° to 16

°C. Fishing is prohibited in the study area.

Sampling of fish and drift

Food consumption was measured on three occasions: 23-28 June, 17-27 July, and 14-19 August. On each occasion, brook charr were collected in 4 h intervals with a backpack electroshocker (Smith-Root 15-C) in each of eight stream sections (four pools, four riffles) closed with a modified seine net (6 mm mesh size). All pool sections were downstream of riffle habitat, and three of the four riffle sections were downstream of pool habitat. Fishing intervals corresponded to different periods of light intensity (dawn: 3:00-7:00; daytime: 7:00-11:00; 11:00-15:00 and 15:00-19:00; dusk: 19:00-23:00; nighttime: 23:00-3:00). Intervals will be designated hereafter by their midpoint, e.g. 5:00 refers to the interval 3:00-7:00.). On each sampling day, fish were collected from one pool and one riffle in each sampling interval. Operators began electrofishing at the downstream end of each section and gradually moved upstream over a 24 h period, avoiding zones fished earlier. Progressive removal of fish by electrofishing similar to that in this study had no effect on short-term behaviour (swimming vs. resting in cover) of the fish that remained in the stream in a study of cutthroat trout, *Oncorhynchus clarki* (Mesa and Schreck 1989). Fish were anesthetized in a solution of MS-222, measured (FL, nearest mm) and weighed (nearest 0.01g). Stomach contents were then extracted by gastric lavage (Light et al. 1983) and preserved immediately in 70% isopropanol. To test the efficacy of extraction, we dissected 57 brook charr that had undergone gastric lavage and examined their stomachs. Gastric

lavage extracted 97.3 ± 1.2 % (mean ± SE) of the wet mass of stomach contents. Following gastric lavage, brook charr were held temporarily in instream tanks; they were then released after the last sampling interval.

Drifting invertebrates were collected over 4 h intervals with a net (mouth opening: 30 cm high x 46 cm wide; 250 μm mesh size) placed in the stream thalweg at the upstream end of each sampled section (4 h intervals in seven sections in June, seven sections in July, eight sections in August). Drift nets were never completely submerged. Drift samples were preserved in 20% formalin. Current velocity (cm s^{-1}) at the mouth of the drift net was measured at the beginning and at the end of each 4 h interval with a Pygmy-type current meter (Scientific Instruments 1205).

In the laboratory, parasites, minerals, and vegetal debris were removed from stomach contents prior to weighing. Individual samples were then filtered, dried at 65°C in an aerated oven for 24 h, and weighed (Mettler AE 200) to the nearest 0.1 mg. For each section, we obtained mass of drifting organisms per 4 h interval as the mean from 3 to 5 subsamples collected from a suspension of drifting material (0.7-1 l) which was homogenized by a stream of air bubbles in a glass cone (Wrona et al. 1982). Subsamples represented about 25% of total drift material. After separating invertebrates from other material, drift subsamples were dried and weighed as described above.

Food consumption and drift biomass estimates

Instantaneous (4 h) and daily (24 h) food consumption was calculated as relative

content mass (RCM; Hyslop 1980) to normalize for differences in fish mass:

$$\text{RCM} = \frac{\text{mg dry mass prey}}{\text{g wet mass fish}}$$

Instantaneous food consumption for each 4 h interval, expressed as RCM 4^{-1} h^{-1}, was calculated following Elliott and Persson (1978):

$$C_t = \frac{(W_f - W_o e^{-Rt})Rt}{1 - e^{-Rt}}$$

where R is the gastric evacuation rate (h^{-1}), W_o is the geometric mean RCM at the beginning of a 4 h sampling interval, and W_f is the geometric mean RCM at the end of the sampling interval. The effects of time of day, month, and habitat type on instantaneous food consumption (non-transformed) were tested by ANOVA.

To avoid bias due to 'lack-of-closure', daily food consumption (C; RCM d^{-1}) was calculated with the bias-corrected Eggers model (Hayward 1991):

$$C = (W_T \cdot R \cdot T) + (W_f - W_o)$$

where R is the gastric evacuation rate (h^{-1}), T is the time between the beginning (t = 0 h) and the end of sampling (20 h in this study), W_o is the geometric mean RCM at the beginning of sampling, W_f is the geometric mean RCM at the end of sampling, and W_T is the geometric mean RCM for all fish captured during the 20 h period (mean = 27.3 fish, range = 24 - 31). The effects of month, habitat, and population densities of brook charr and Atlantic salmon on daily food consumption (non-transformed) were tested by ANCOVA.

We estimated gastric evacuation rates on the field 1 week prior to fish sampling. Although conditions instream are not controled (water temperature, turbidity, etc.), field

estimation can underpass the potential problems of laboratory experiments, like single-meal designs based on one type of prey (Bromley 1994). In 1994 and 1995 fish (13 - 31 per trial) were collected by electrofishing and kept at low densities in instream tanks with constant flow of filtered (450 μm mesh) water. Stomach contents of 4 to 7 fish (mean = 5.4) were extracted in each of 3 to 6 occasions evenly spaced over a 20 h period. Gastric evacuation rates were estimated with the equation:

$$\ln W_t = b_0 + b_1 \ln W_f + R \cdot t$$

where t is the time spent without feeding, W_t is the mean dry mass of prey (mg) for fish at a given t, b_0 and b_1 are constants, W_f is the mean wet mass of fish (g) at a given t, and R is the gastric evacuation rate (h^{-1}). There was no significant effect of habitat type ($p = 0.08$), temperature ($p = 0.26$) or their interaction ($p = 0.06$) on gastric evacuation rate (ANCOVA with habitat and temperature as main factors). Therefore, the grand mean of gastric evacuation rates (0.096 h^{-1}; Table 1) was used in calculating consumption. This estimate of gastric evacuation rate is similar to those obtained in other studies on brook charr (0.104 h^{-1} for brook charr in Lake Simpson, Canada, Héroux and Magnan 1996; 0.051 to 0.112 h^{-1} in Matamek River, Canada, Walsh et al. 1988).

Relative body condition (K_n) was calculated as $K_n = W / W'$, where W is the wet mass (g) of an individual and W' is the length-specific wet mass predicted by an allometric mass-length equation for the population. A value of one indicates average condition (Anderson and Neuman 1996). The effects of month and habitat on relative body condition (non-transformed) were tested by ANOVA.

Drift biomass (mg DM m^{-2} s^{-1}) and drift abundance (number m^{-2} s^{-1}) were calculated as drift passing through a "foraging area" of 1 m^2 cross-section per second (Fausch 1984). The influence of time of day, month, and habitat type on drift biomass per 4 h interval (log-transformed) was examined with ANOVA. We estimated the mean amount of drift available to fish during the day (daytime drift biomass) by averaging drift biomass for the intervals corresponding to dawn, daytime, and dusk (5:00 to 21:00). The nighttime interval (23:00-3:00) was excluded because food consumption was negligible at that time (see Results). The effects of month and habitat type on variation in daytime drift biomass (log-transformed) were tested with ANOVA. Mean mass of individuals in the drift (mg DM) was obtained by dividing total mass by number of individuals.

Population densities

We estimated densities (number per 100 m^2) of brook charr and Atlantic salmon approximately one week prior to evaluating food consumption. A minimum of three electrofishing passes in an upstream direction were done in closed stream sections. Fish were assigned to age-classes (0+, 1+, and $\geq$ 2+) based on length-frequency distributions. Densities were estimated separately for each species and age-class by the removal method (Rexstead and Burnham 1991). Differences in biomass of brook charr (charr density x mean individual charr weight; log-transformed) between pools and riffles were examined separately for each month with paired t-tests.

Results

Instantaneous food consumption by brook charr showed significant daily variation (Table 2). No effect of month or habitat type was detected. The daily pattern of food consumption was strongly unimodal (Fig. 1), with a peak near 13:00 (mean ± SE; 1.472 ± 0.303 RCM 4^{-1} h^{-1}) and negligible consumption at 1:00 (0.012 ± 0.249 RCM 4^{-1} h^{-1}). The difference between the two periods is statistically significant (Tukey post-hoc comparison, $p=0.02$).

Daily food consumption declined markedly over the summer (Fig. 2; Table 3). Food consumption did not differ significantly between pools and riffles, and was not significantly influenced by densities of conspecifics or heterospecifics (Table 3). Relative condition factor of brook charr was 1.01 ± 0.01 (mean ± SE) in June. Condition did not change significantly in July (1.03 ± 0.02), but it decreased significantly (0.97 ± 0.01) in August (ANOVA with month and habitat as main factors; Tukey post-hoc comparisons) (Fig. 3). Relative condition factor did not differ significantly between pools and riffles. Mean biomass of brook charr was significantly higher in pools than in riffles in July and August (Table 4). Mean biomass of brook charr was 2.8 times greater in pools than in riffles in June, a difference that became more marked in July (4.2 times) and August (6.4 times).

Drift biomass showed marked daily variation (Fig. 4; Table 5). Drift biomass decreased significantly from 1:00 to 5:00 (Tukey post-hoc comparison; $p < 0.001$); did not change significantly from 5:00 to 17:00 (Tukey post-hoc comparisons; $p > 0.05$ for all comparisons between adjacent time intervals); and then increased significantly at dusk

(17:00 to 21:00, $p < 0.001$). Drift biomass was significantly higher at 1:00 than at 21:00 ($p < 0.001$). Drift biomass in pools was on average 2.2 times higher than in riffles ($p < 0.001$; Table 5). The magnitude of this difference between habitats did not vary significantly over the day or the season (Fig. 4; Table 5).

Daytime drift biomass did not vary significantly over the summer (Fig. 5; Table 6). Daytime drift biomass was significantly higher in pools (mean ± SE; 0.22 ± 0.06 mg DM m^{-2} s^{-1}) than in riffles (0.09 ± 0.02 mg DM m^{-2} s^{-1}) (Fig. 5; Table 6). Apparent seasonal constancy in daytime drift biomass masked marked seasonal variation in individual prey mass. Individual prey mass in drift (excluding the nighttime interval) declined significantly during the summer, but did not differ between habitats (Fig. 6; Table 7). No significant seasonal change was detected in numbers of drifting prey (ANOVA with month and habitat as main factors, $p > 0.05$).

Discussion

The results show that feeding by brook charr peaked at midday and was negligible at night. Daily food consumption declined over the summer, concomitant with a decrease in individual body mass of drifting prey. Food consumption expressed as a proportion of fish mass did not differ in pools and riffles, but total charr biomass, and thus total food consumption, was considerably higher in pools than in riffles. The abundance of potential conspecific or heterospecific competitors had no apparent effect on food consumption.

Although there is some evidence of feeding by salmonids after sunset (Jenkins 1969;

Fraser et al. 1993), food consumption generally peaks during daytime or at dawn or dusk (e.g. Brodeur and Pearcy 1987; Sagar and Glova 1988; Walsh et al. 1988; Angradi and Griffith 1990). The daily feeding peak in this study occurred at midday, when drift biomass was at its lowest. Even though salmonids can see prey and feed at low light levels, efficiency at capturing drifting prey declines with falling light levels (Wilzbach et al. 1986; Young et al. 1997), perhaps explaining why food consumption by brook charr was low at night, dawn, and dusk. Field observations of brook charr show that activity in summer is generally low at nighttime, when fish tend to remain motionless on the stream bottom (Walsh et al. 1988; A. Guitard, pers. observ.).

Food consumption declined progressively from June to August. Decline in food consumption by stream-dwelling brook charr over the summer has been reported earlier (e.g. Gibson et al. 1984; Walsh et al. 1988), and has been related to seasonal variation in drift abundance. In temperate regions, summer is the main period of growth for most stream insects and fish. In late spring and early summer, organic material released as fallen leaves decompose accelerates growth of aquatic insects (mostly larval stages), which later emerge in high numbers throughout the summer (Allan 1995; Schlosser 1995). Emergence of adults reduces the instream abundance (Wipfli 1997) and the mean size of aquatic insects (Egglishaw 1967); food availability for salmonids may thus decline over the summer (Hearn 1987; Power 1993).

Although in the present study daytime drift biomass did not show significant seasonal change, mean mass of individual prey (and presumably energetic content per prey) in drift

decreased significantly over the summer. Salmonids capture prey selectively relative to size composition of prey in drift (Bannon and Ringler 1986; Grant and Noakes 1986). Profitability (net energetic return) of prey in drift increases with prey size up to a limit, generally set by handling constraints; profitable prey typically are larger than the mean size of drifting prey (Grant and Noakes 1986). The seasonal decline in individual mass of prey in drift may thus lead to reduction in abundance of profitable prey. In June, mean mass of individual prey is high and large prey are abundant. In August however, brook charr might ignore abundant small prey and capture only profitable larger prey in drift; overall capture rate would then be lower.

Daily food consumption (% of body DM d^{-1}) in this study was 1.94 % in June, 1.50 % in July, and 1.12 % in August, assuming brook charr dry mass equals 0.24 x wet mass (Elliott 1975). Rainbow trout, *Oncorhynchus mykiss*, in Idaho, consumed 2% DM d^{-1} in June, 1.8% in July, and 1.9% in August (Angradi and Griffith 1990). Juvenile chinook salmon, *Oncorhynchus tshawytscha*, in New Zealand consumed 8.3% DM d^{-1} in November (austral summer) (Sagar and Glova 1988). Brook charr in Stoney Brook, New Hampshire (Forrester et al. 1994) consumed 1.75% DM d^{-1} in August. Food consumption by brook charr was highly variable in Matamek River (7.13% DM d^{-1} in June, 9.75% in July, and 1.27% in August) and Rivière à la Truite (5.09% in July and 4.09% in August) in Quebec, Canada (Walsh et al. 1988). Estimates of daily food consumption of 4.4 - 6.6 DM d^{-1} have been interpreted as indicating food limitation in juvenile estuarine or marine salmonids (see Sagar and Glova 1988). Forrester et al. (1994) concluded that low food consumption

(1.75% DM d^{-1}) suggested that food was not superabundant in August. In the present study, the reduction in food consumption over the summer and the decline in relative condition factor in August may thus reflect a late summer food deficit.

Habitat type and population densities of conspecifics and heterospecifics appeared to have no effect on daily food consumption and condition factor by brook charr, in agreement with Forrester et al. (1994), who found no difference in food consumption by brook charr individuals maintained at population densities lower (0.88 m^{-2}) and higher (1.56 m^{-2}) than the natural mean density (1.2 m^{-2}). Movement of fish between habitats during sampling cannot explain similar food consumption by charr in the two habitats because sections were closed with seine nets. Interhabitat movement of brook charr between sampling dates could mitigate possible differences in condition factor between pools and riffles. However, for brook charr exchange of individuals between habitats appears to be limited in this system (Dussault 1995).

Although in the present study food consumption per unit fish mass was similar in pools and riffles, brook charr biomass was considerably higher in pools than in riffles, and thus total food consumption by brook charr was higher in pools than in riffles. Low-velocity habitats such as pools act as retention basins where drifting prey items sink and accumulate (McLay 1970). Other physical characteristics of pools, such as low surface turbulence, which facilitates capture of insects at the water surface (Egglishaw 1967), or small substratum particles which limit hiding spaces for insect prey (Wilzbach et al. 1986), may further enhance prey availability in pools, in agreement with earlier work showing that

higher biomass of brook charr is maintained in pools than in riffles (Gibson et al. 1993).

In this study system, a theoretical model of habitat selection based on ideal distribution assumptions, provided an excellent fit to observed densities in pools and riffles in an earlier study (Rodríguez 1995), thus supporting the basic tennet that individual profitability is equalized across habitats. The findings in the present study that (1) brook charr biomass is higher in pools than in riffles; (2) food consumption per unit mass is similar in the two habitats; (3) population density of conspecifics and heterospecifics are unrelated to food consumption are consistent with the notion that for brook charr pools are intrinsically more profitable habitat than riffles, but that population densities in the two habitats are indeed adjusted so as to equalize individual profitability across habitats.

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Table 1. Gastric evacuation rates for brook charr in pools and riffles. Evacuation rates (R) were estimated with the model: $\ln W_t = b_0 + b_1 \ln W_i + R \cdot t$ (see text for details). The significance value for the effect of time, p_{time} is shown also.

Date	Number of fish	Fish body weight, g (mean ± SE)	Mean temperature, °C	Evacuation rate, R (h^{-1})	p_{time}
Pools					
2 July 1994	29	12.1 ± 2.7	15.2	0.100	< 0.001
7 June 1995	22	3.8 ± 1.9	12.5	0.081	0.001
5 July 1995	20	6.0 ± 1.6	14.3	0.115	0.001
6 Aug. 1995	31	8.8 ± 1.6	15.0	0.116	< 0.001
Riffles					
30 June 1994	25	5.1 ± 1.6	16.0	0.083	0.001
28 July 1994	41	3.2 ± 0.9	15.3	0.087	0.001
5 July 1995	22	2.5 ± 0.4	11.3	0.100	0.018
3 Aug. 1995	13	1.1 ± 0.1	13.3	0.089	0.001

Table 2. ANOVA examining the effects of temporal variation (time of day, month) and habitat type (pools and riffles) on instantaneous food consumption of brook charr (mg DM prey per g WM fish 4^{-1} h^{-1}; n = 120 time intervals).

Effect	df	F-ratio	p
Time of day	5	2.72	0.02
Month	2	0.24	0.78
Habitat	1	0.02	0.88
Error	111		

No significant interactions were found in the analysis

Table 3. ANCOVA examining the effects of month, habitat type (pools and riffles), and potential competitors on daily food consumption of brook charr (mg DM prey per WM fish day^{-1}; n = 24 daily estimates).

Effect	df	F-ratio	p
Month	2	4.30	0.03
Habitat	1	0.88	0.36
ln (Density of charr)	1	0.06	0.81
ln (Density of salmon)	1	3.09	0.10
Error	18		

No significant interactions were found in the analysis

Table 4. Biomass of brook charr (g WM per 100 m^2; mean ± SE) in pools and riffles, by month. Significance values of paired t-tests for habitat differences are reported also (n = 6 pool-riffle pairs).

Month	Pools	Riffles	p
June	77 ± 32	28 ± 8	0.09
July	290 ± 116	69 ± 23	0.048
August	718 ± 220	112 ± 56	0.009

Table 5. ANOVA examining the effects of temporal variation (time of day, month) and habitat type (pools and riffles) on drift biomass (mg DM $m^{-2} s^{-1}$; n = 132 time intervals).

Effect	df	F-ratio	p
Time of day	5	33.81	< 0.001
Month	2	6.46	0.002
Habitat	1	22.29	< 0.001
Error	123		

No significant interactions were found in the analysis

Table 6. ANOVA examining the effects of month and habitat type (pools and riffles) on daytime drift biomass (mg m^{-2} s^{-1}; n = 22 daily estimates).

Effect	df	F-ratio	p
Month	2	0.88	0.43
Habitat	1	7.08	0.02
Error	18		

The month by habitat interaction was not significant.

Table 7. ANOVA examining the effects of month and habitat type (pools and riffles) on individual prey mass (DM, mg) in drift (n = 22 daily estimates).

Effect	df	F-ratio	p
Month	2	8.10	0.003
Habitat	1	2.68	0.12
Error	18		

The month by habitat interaction was not significant.

Figure captions

Figure 1. Daily variation in food consumption by brook charr. Means are plotted at the midpoint of each time interval. Nighttime: filled circles; dawn or dusk: shaded circles; daytime: empty circles. Vertical lines represent ± SE.

Figure 2. Seasonal change in daily food consumption by brook charr. Vertical lines represent ± SE.

Figure 3 Seasonal change in relative condition factor of brook charr. Vertical lines represent ± SE.

Figure 4. Daily variation in drift biomass in pools (circles) and riffles (squares). Geometric means are plotted at the midpoint of each time interval. Shading of symbols for nighttime, dawn, dusk, and daytime as in Fig. 1. Vertical lines represent ± SE, back-calculated from log-transformed data.

Figure 5. Seasonal variation in daytime drift biomass. Geometric means are plotted at the midpoint of each month. Pools: circles; riffles: squares. Vertical lines represent ± SE, back-calculated from log-transformed data.

Figure 6. Seasonal variation in drift numerical abundance (squares) and mean mass of individual prey (circles). Vertical lines represent ± SE. SE for mean mass of individual prey was back-calculated from log-transformed data.

Figure 1

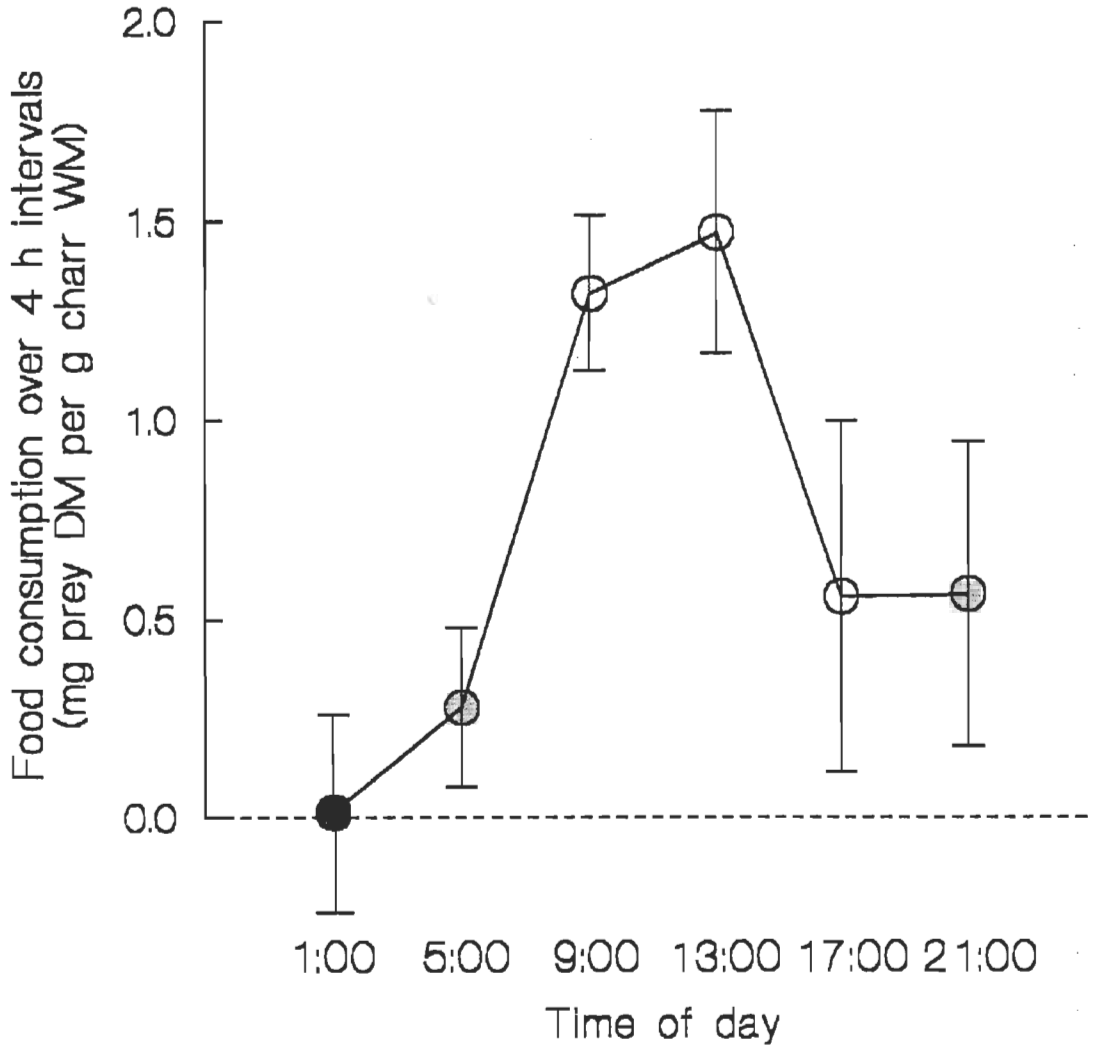

Food consumption over 4 h intervals
(mg prey DM per g charr WM)
2.0
1.5
1.0
0.5
0.0
1:00
5:00
9:00
13:00
17:00
21:00
Time of day

Figure 2

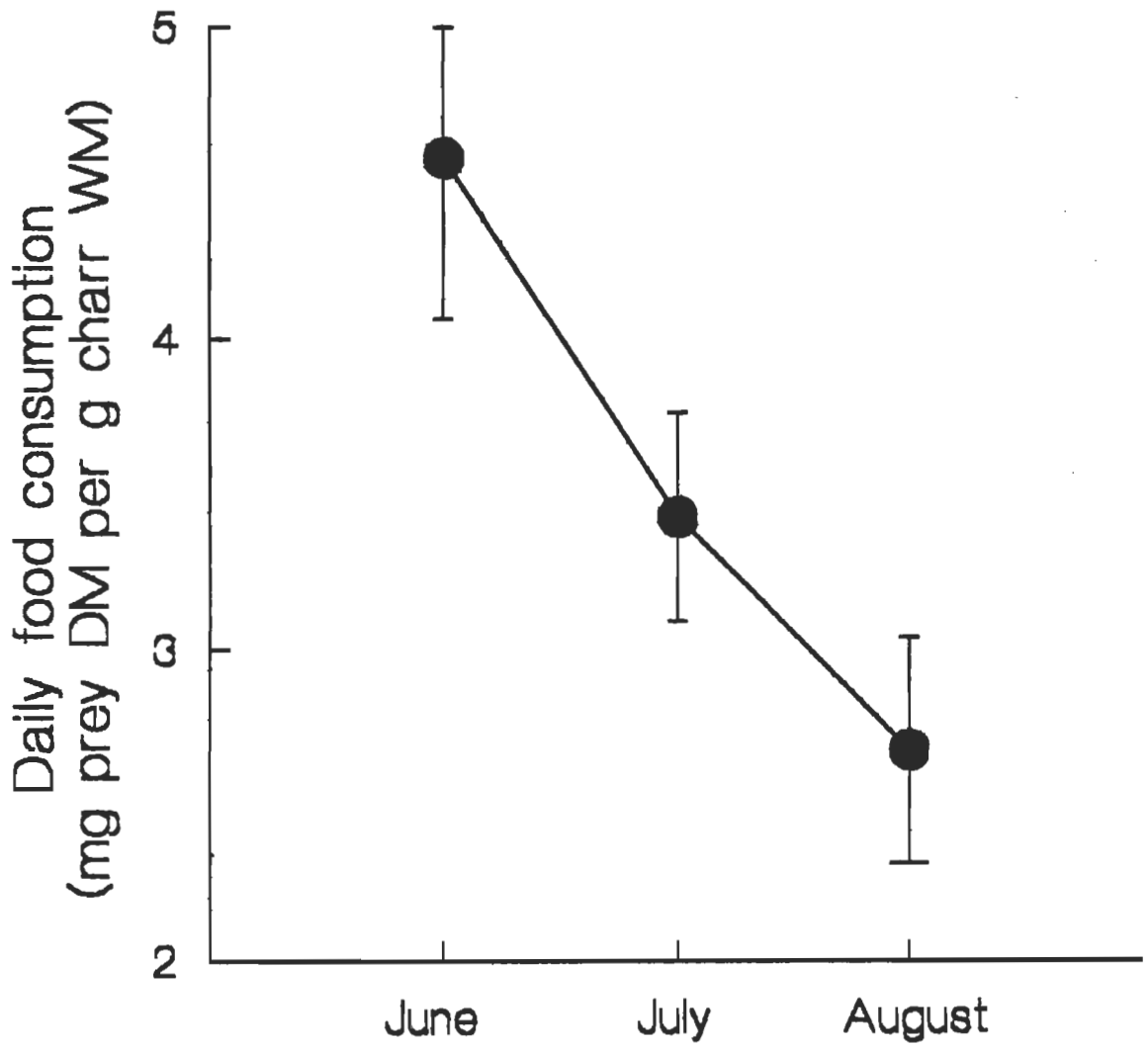

Daily food consumption
(mg prey DM per g charr WM)
5
4
3
2
June
July
August

Figure 3

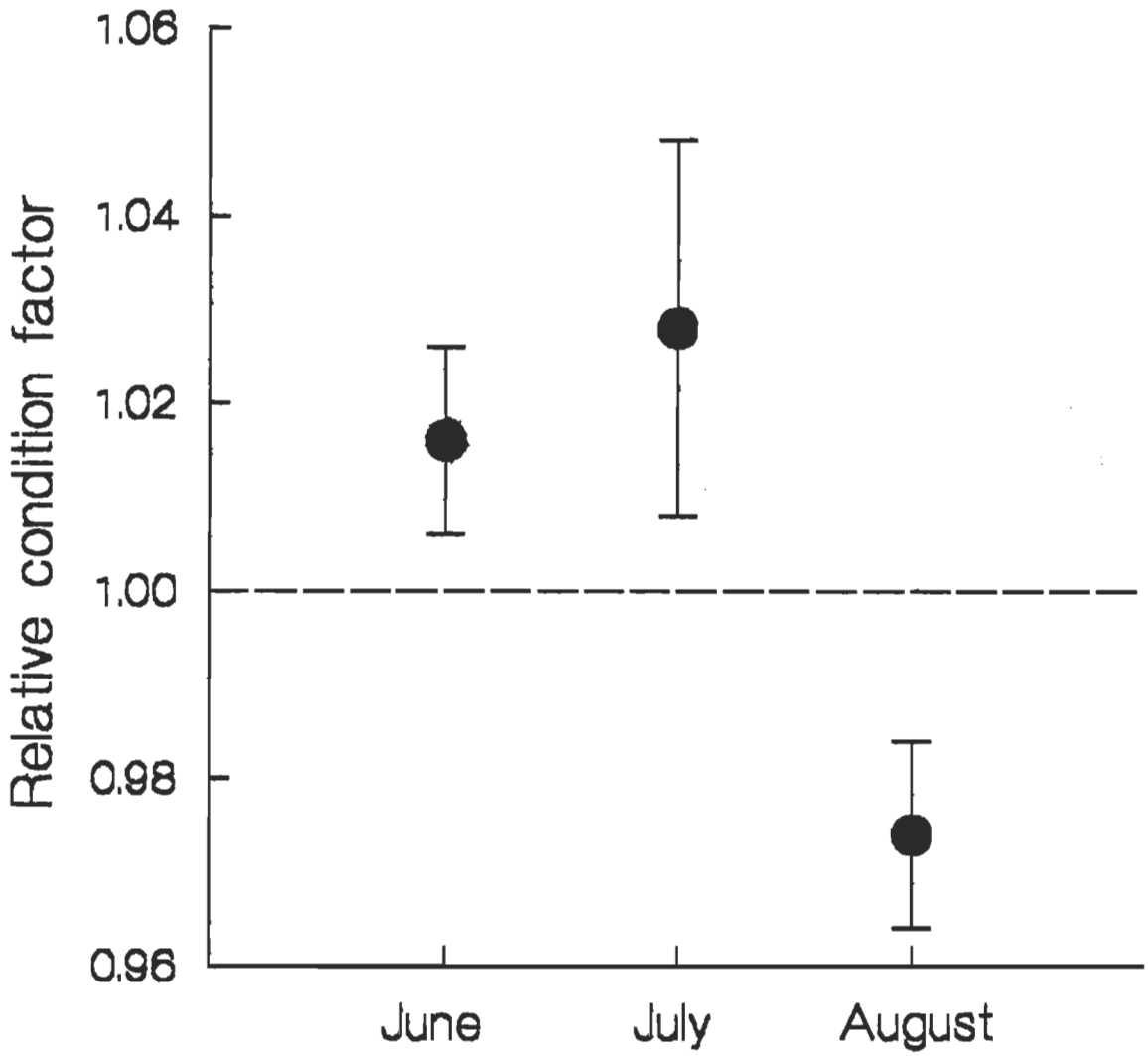

Relative condition factor
1.06
1.04
1.02
1.00
0.98
0.96
June
July
August

Figure 4

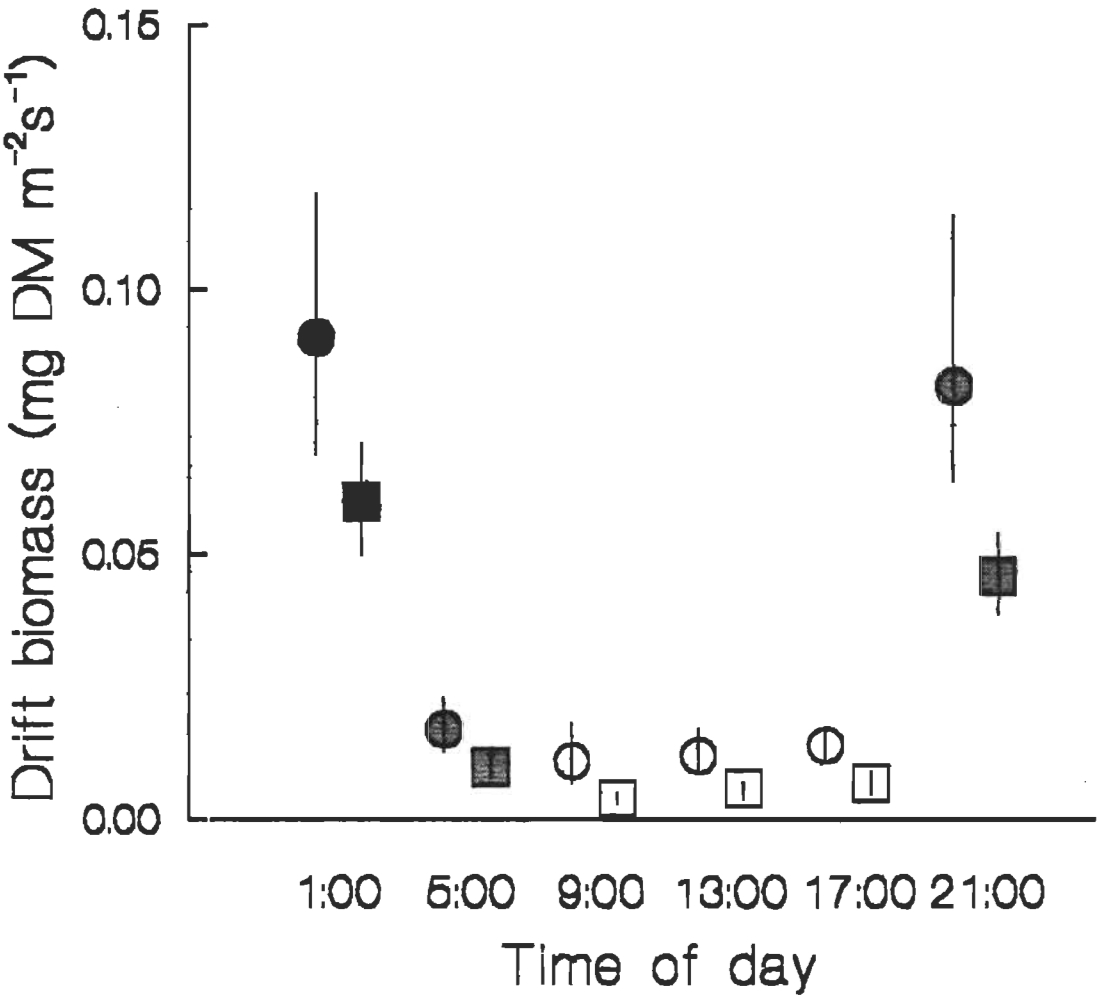

0.15
0.10
0.05
0.00
Drift biomass (mg DM m-2s-1)
1:00
5:00
9:00
13:00
17:00
21:00
Time of day

Figure 5

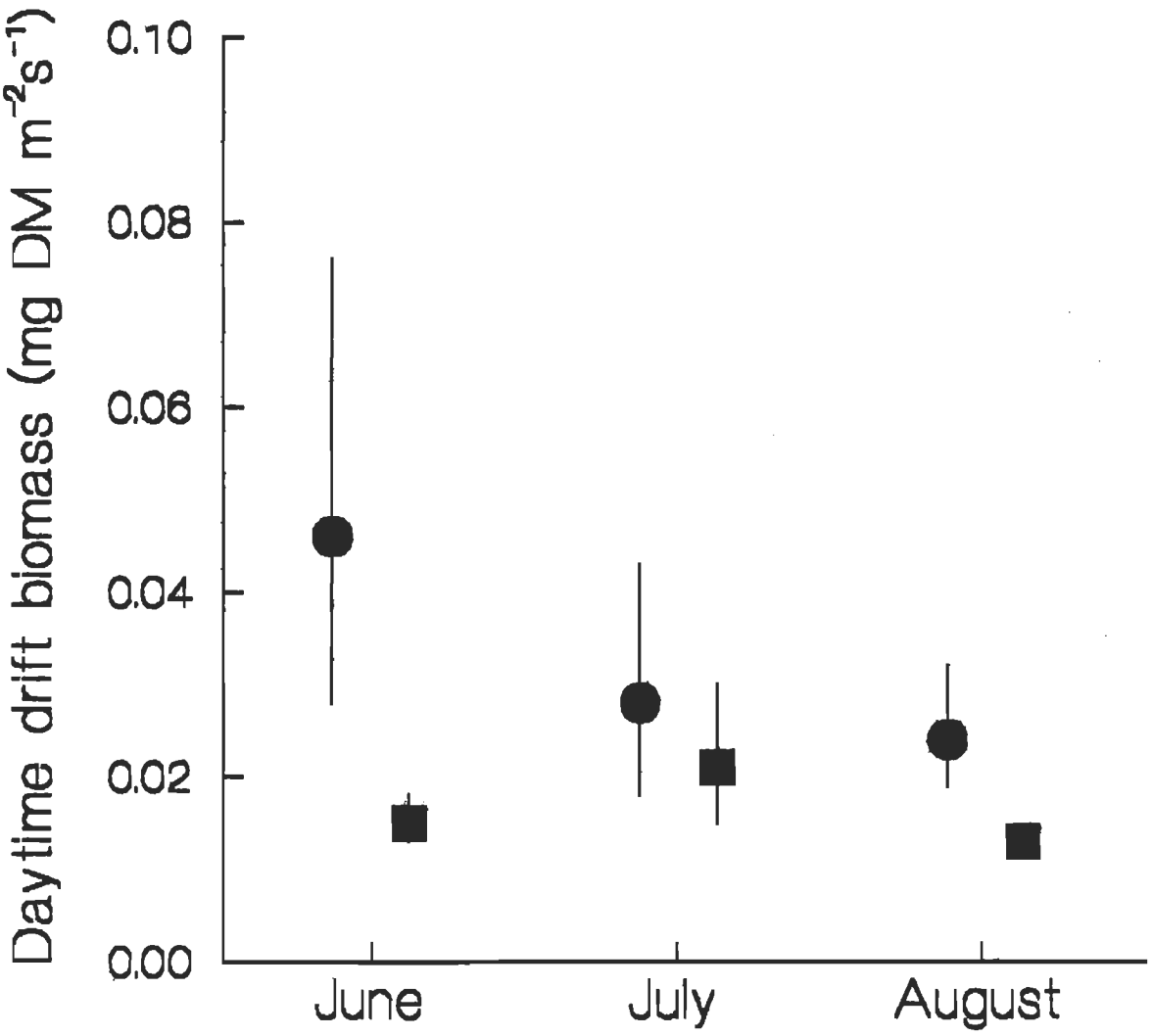
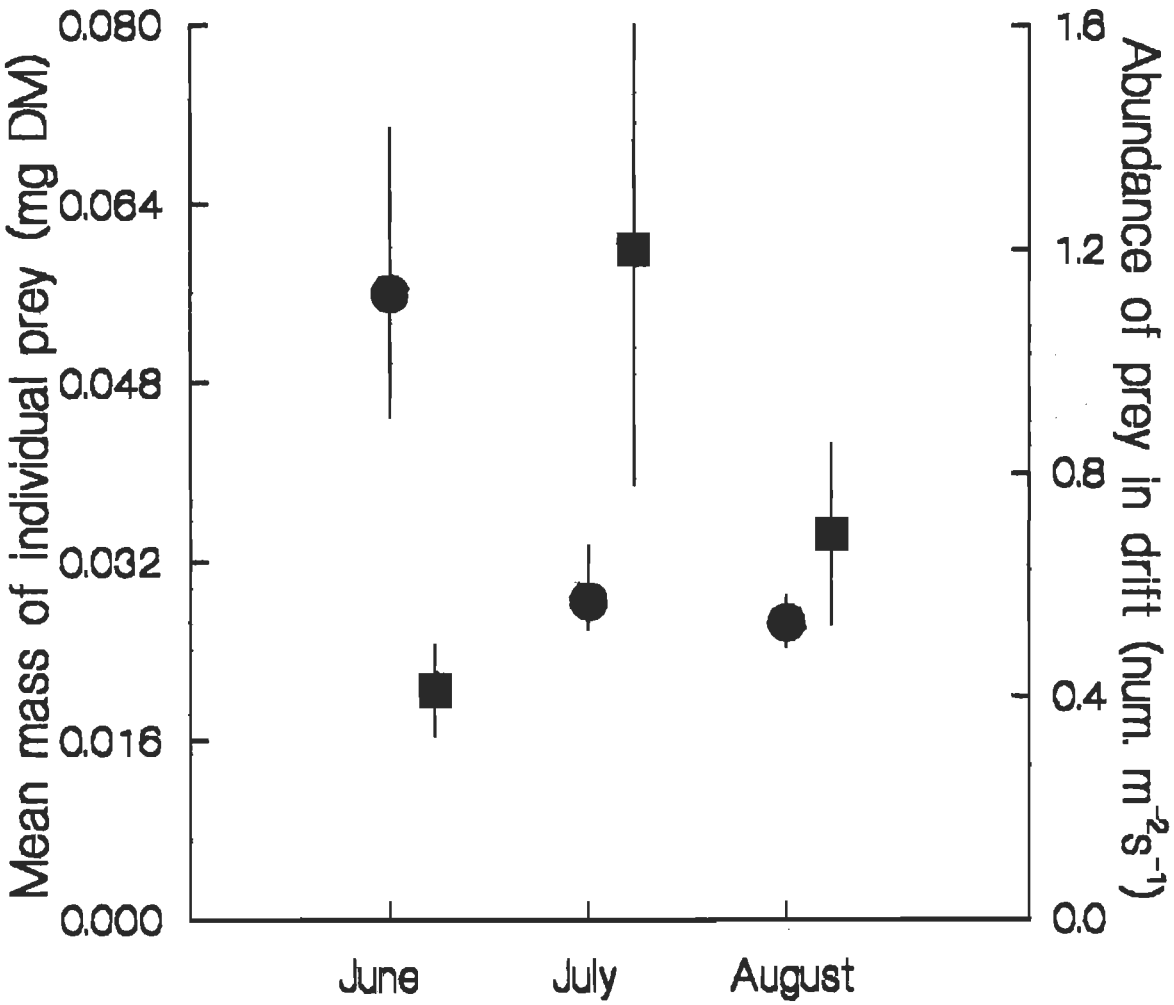

Daytime drift biomass (mg DM m^{-2}s^{-1})
0.10
0.08
0.06
0.04
0.02
0.00
June
July
August

Figure 6


Mean mass of individual prey (mg DM)
0.080
0.064
0.048
0.032
0.016
0.000
Abundance of prey in drift (num. m-2s-1)
1.6
1.2
0.8
0.4
0.0
June
July
August

CHAPITRE II

DIETARY VARIATION IN STREAM-DWELLING BROOK CHARR AND JUVENILE ATLANTIC SALMON: INTERACTIVE EFFECTS OF SEASON, HABITAT, AND POPULATION DENSITIES.

Abstract. This study examined how diversity, overlap, and taxonomic composition of brook charr, *Salvelinus fontinalis*, and juvenile Atlantic salmon, *Salmo salar*, diets varied in relation to seasonal change (June, July, and August), habitat type (pools and riffles), and population densities (conspecific and heterospecific) in small streams of eastern Quebec. Detrended correspondence analysis (DCA) showed that brook charr consumed more terrestrial prey and less aquatic prey than Atlantic salmon. Atlantic salmon had a less diverse diet in riffles than in pools. Brook charr dietary diversity varied seasonally and was lowest in August, as was the dietary overlap between the two species. Canonical correspondence analyses (CCA) revealed significant effects of seasonal variation and heterospecific densities on dietary composition for both brook charr and Atlantic salmon; dietary composition of Atlantic salmon also was influenced by habitat. Consumption by brook charr of dipteran adults, its most important prey, was influenced by a strong interaction between season and salmon density. Atlantic salmon reduced consumption of its principal prey item, ephemeropteran larvae, with increases in charr density. In addition to the seasonal changes often analyzed in studies of fish diet, the results illustrate the advantages of examining the effects of habitat and heterospecifics, as well as the potential interactions between these factors.

Introduction

Variation in fish diet often is described with reference to seasonal change (Angermeier 1982; Magalhaes 1993), inter-habitat differences (Bridcut and Giller 1993), and presence or absence of potential competitors (Persson 1986; Bergman 1990). Very few studies have examined possible interactions among these factors (e.g. habitat and season: Holbrook and Schmitt 1989; habitat and intraspecific competitors: Holbrook and Schmitt 1992; habitat, season, and intraspecific competitors: Diehl 1993). Field studies of interactive effects require large sample sizes because dietary data must be obtained in different habitats over at least one season, under various combinations of presence-absence or abundance of potential competitors. Stream-dwelling salmonids provide good opportunities for evaluating possible interactive effects of seasonal variation, habitat, and competitors on fish diet. In northern streams, food resources generally decline over the summer, the main growing period for fish (Angermeier 1982). Diet in stream salmonids can differ in contrasting habitats (Egglishaw 1967, Nielsen 1992). It is common to find in the same stream two or more salmonid species with broadly overlapping diets (Power 1980; Thonney and Gibson 1989), which favors the occurrence of interspecific competition when food abundance is low (Hearn 1987).

Brook charr, *Salvelinus fontinalis*, and Atlantic salmon, *Salmo salar*, often are found in sympatry in small streams of eastern Canada (Gibson et al. 1993). Spatial segregation during the summer has been documented in these two species. In allopatry, both brook charr and Atlantic salmon utilize riffle habitats, but in sympatry, salmon displace charr to pool

habitats (Gibson 1973, 1978, Gibson et al. 1993, Rodríguez 1995). Although some studies have examined dietary composition in brook charr and Atlantic salmon (Williams, 1981; Gibson et al. 1984; Thonney and Gibson 1989) including the role of seasonal variation and interspecific competition, possible interactions between season, habitat, and potential competitors have rarely been evaluated.

This study examines the effects of summer seasonal variation (June, July, and August), habitat type (pools and riffles), and population densities of conspecifics and heterospecifics on the diversity, overlap, and taxonomic composition of diets of stream-dwelling brook charr and juvenile Atlantic salmon. The significance of interactions between season, habitat, and population densities is also considered.

Materials and methods

The study was conducted in Gunn Creek and Chandler Creek, in the Matapedia Valley, eastern Quebec, Canada (Table 1). Two different sites, separated by 1.2 km, were studied in Gunn Creek. Brook charr and Atlantic salmon are sympatric at the downstream site (South Gunn), whereas brook charr is generally the only species found at the upstream site (North Gunn). Brook charr and Atlantic salmon are numerically dominant species in Chandler Creek; longnose dace, *Rhinichthys cataractae*, and slimy sculpin, *Cottus cognatus*, are present at low densities. Fishing was prohibited in the study area.

Fish were sampled at daytime (8:00 to 19:00) with a backpack electroshocker (Smith Root 15-B) in late June (23-30 June), mid-July (17-27 July), and mid-August (14-19

August) of 1995. Sampling occured in 12 sections in June, 10 sections in July, and 14 sections in August (Table 1). Fish were collected from one pool and one riffle on each sampling day. Fish were anaesthetized in a tricaine solution (MS-222; 50-60 mg/L), measured (FL; mm), and weighed to the nearest 0.1 g (electronic field balance). Stomach flushing was performed following Light et al. (1983). This procedure seemingly has little effect on feeding, body condition, and survival in salmonids (Meehan and Miller 1978; Twomey and Giller 1990). After stomach flushing, fish were kept in instream tanks for periods ranging between 4 and 11 h, and were released in the stream locality where they were captured. Mortality between stomach flushing and release (0 % for salmon, n=151 fish; 1.0 % for charr, n=411 fish) was negligible. Stomach contents were preserved in 70% isopropanol and fish rested for at least 1 hour in instream tanks to permit full recovery. Measuring, weighing, and stomach flushing generally required less than one minute per fish (mean ± SD; 44.0 ± 10.0 s). Dissection of fish (a subsample of 57 charr and 31 salmon) following gastric lavage showed that almost all prey (numerical abundance; brook charr: 98.8 %; Atlantic salmon: 99.5 %) had been extracted by gastric lavage. In the laboratory, 47 distinct prey items were identified with a binocular microscope (Leica MS5) to order and life stage, but larval aquatic dipterans were identified to family.

Population densities (numbers per 100 m^2) of brook charr and Atlantic salmon were obtained by electrofishing in each stream section approximately one week before collection of stomach contents. Individual sections were closed with block nets; then, a minimum of three fishing passes were done starting at the downstream net and moving upstream. Fish

densities were estimated separately for each species and age-class (removal method; Rexstead and Burnham 1991).

We assessed age-related differences in dietary composition for the two species with detrended correspondence analyses (DCA CANOCO program version 3.1, ter Braak 1990), an eigenvector ordination technique. Brook charr (age 0+: mean FL, 45 mm, 70.5% by numbers; age 1+: mean FL, 82 mm, 24.8% by numbers) and Atlantic salmon (age 1+: mean FL, 62 mm, 44% by numbers; age 2+: mean FL, 83 mm, 56% by numbers) were grouped by age and section. The mean relative abundance (% numbers) of each prey item was obtained by pooling across all individuals by age and section. Sections with less than three fish were excluded from the analysis. Brook charr of age 2+ and older were excluded from the analysis above because of their low abundance in fish samples (4.7 %). The DCA ordinations showed no distinct pattern of dietary differentiation by age for brook charr or Atlantic salmon.

Dietary diversity of brook charr and Atlantic salmon was quantified for individual sections with the reciprocal of Simpson's dominance index (1/D; i.e. Simpson's diversity), modified for a finite number of prey items (Magurran 1988):

$$\frac{1}{D} = \frac{1}{\sum_i \frac{(n_i)(n_i - 1)}{(N)(N - 1)}}$$

where n_i is the number of prey of taxon i, pooled across all stomachs, and N is the total number of prey. Simpson's diversity could vary between 1 (only one prey type) and 47 (all taxa equally represented) in this study. The effects of season, habitat type, and population densities on dietary diversity were evaluated with analysis of covariance (ANCOVA). For

each species, sections with less than three fish were excluded from the analysis.

Dietary overlap of brook charr and Atlantic salmon was quantified for individual sections with Pianka's index (Pianka 1973):

$$a_{j,k} = \frac{\sum_i (p_{ij} \times p_{ik})}{\sqrt{(\sum_i p_{ij}^2 \times \sum_i p_{ij}^2)}}$$

where p_{ij} and p_{ik} are the proportion of prey taxon i used by species j or k. For each fish species, proportions were based on numerical abundances, pooled across all individuals in a section. This index ranges from 0 (no overlap) to 1 (identical diet). Sections with less than six fish of each species (mean ± SD; 8.0 ± 1.4) were excluded from the analysis.

Detrended correspondence analysis was used to assess the extent of intra- and interspecific variation of dietary composition (% numbers) in brook charr and Atlantic salmon. For this analysis, prey taxa were regrouped into 26 categories (Table 2).

Canonical correspondence analysis (CCA, CANOCO program, version 3.1, ter Braak 1990) was used to examine how dietary composition of brook charr and Atlantic salmon varied in relation to season, habitat type, and population densities. The forward selection procedure implemented in CANOCO was used to eliminate variables that did not significantly influence dietary variation. A threshold p value of 0.05 was used in variable selection. Significance tests for the effects of season, habitat type, and population densities in the final models were obtained with Monte Carlo tests (1000 permutations) for the sum of all eigenvalues (pSum), and for the first (pAxis 1) and second (pAxis 2) canonical axes. The significance of canonical coefficients was tested with approximate t-tests at α = 0.05 (ter

Braak 1990). CCA models the collective response of all prey taxa to the main effects of season, habitat, and population densities. However, responses of single taxa can be represented more precisely by use of taxon-specific models (ter Braak and Prentice 1988). Therefore, ANCOVA was used to examine the main effects and interactions of season, habitat, and potential competitors on the relative abundance of the most abundant prey taxa, transformed as arcsin $\sqrt{p}$. However, sample sizes for some cells were too small to estimate the full ANCOVA model for Atlantic salmon. Two approaches were used to sidestep this problem. First, the full ANCOVA model was estimated after excluding sections from July, the month with the lowest sample size. Second, all samples were used to estimate a reduced ANCOVA model that included all main effects and two-way interactions but excluded the three-way interaction. Because substantive conclusions are similar for the two approaches, ANCOVA results are presented only for the first one. In all quantitative analyses, population densities of fish were transformed as ln (x + 1) to satisfy statistical assumptions.

Results

A total of 372 brook charr (mean FL ± SD: 60.0 ± 29.0) and 143 Atlantic salmon (mean FL ± SD: 83.0 ± 23.8 mm) were used in dietary analyses. The mean number of prey per stomach was 18.5 ± 7.8 (mean ± SD) for brook charr and 24.5 ± 15.2 (mean ± SD) for Atlantic salmon. For either species, the mean number of prey per stomach did not change over the summer or between habitats (two-way ANOVA with season and habitat as main factors, $p > 0.05$). Terrestrial prey, particularly adult dipterans, were better represented in

the diet of brook charr than in the diet of Atlantic salmon (Fig. 1). The main prey items in the diet of brook charr were adult dipterans, and larval chironomids, ephemeropterans, and trichopterans (Fig. 1). For Atlantic salmon, the major prey items were larval ephemeropterans, chironomids, simuliids, and trichopterans (Fig. 1). Overall differences in dietary composition between habitats were small relative to interspecific differences (Fig. 1).

Dietary diversity of brook charr showed significant seasonal variation (Fig. 2; Table 3); dietary diversity was significantly lower in August than in June or July (post-hoc Tukey multiple comparison, $p < 0.05$). Dietary diversity of Atlantic salmon was lower in riffles than in pools but showed no significant seasonal variation (Fig. 2; Table 3). No significant effects of habitat type or population densities were detected on dietary diversity of brook charr or Atlantic salmon. Dietary overlap between brook charr and Atlantic salmon, as expressed by Pianka's index ($a_{j,k}$), declined significantly over the summer (Fig. 3; Table 4). Dietary overlap was lowest late in summer; of eight sections that had overlap values smaller than 0.45, seven were from the August samples. Overlap was significantly lower in August than in June or July (Tukey post-hoc comparisons, $p < 0.05$). The absence of a significant season by habitat interaction (Table 4) suggests that seasonal change in overlap was comparable in pools and riffles. Neither habitat type or population densities had a significant effect on dietary overlap (Table 4).

Ordination of dietary samples and prey items in a DCA biplot showed that brook charr and Atlantic salmon diets could be clearly distinguished on the basis of relative abundances of terrestrial and aquatic prey (Fig. 4). DCA axis 1 contrasts diets rich in

terrestrial items, with low values along the axis (left of dashed line: all 11 terrestrial prey), from those rich in aquatic items, with higher values along the axis (right of dashed line: no terrestrial prey) (Fig. 4). Most brook charr samples (28 out of 32 sections) fall to the left of the dashed line; conversely, most Atlantic salmon samples (21 out of 22 sections) fall to the right of the dashed line.

Canonical correspondence analyses revealed significant effects of seasonal variation and heterospecific densities on dietary composition for both brook charr and Atlantic salmon (Table 5). No effect of conspecific density was detected for either species. Habitat had no significant influence on dietary composition for brook charr. For Atlantic salmon, habitat was retained as a significant variable by the forward selection procedure, but this effect is likely minor because habitat differences contribute mostly to the second axis (non-significant: pAxis 2 > 0.05) (Fig. 6; Table 5).

The CCA ordination for brook charr (Fig. 5) illustrates two major trends in dietary composition: (1) a shift (along axis 1) from consumption of chironomid larvae (the second most abundant prey; Fig. 1) to dipteran adults (the most abundant prey) as salmon densities increases; (2) a seasonal shift (along axis 2) from consumption of ephemeropteran larvae (the third most abundant prey), trichopteran larvae (fourth), and many secondary prey of low abundance in June and July, to consumption of the two most abundant prey, dipteran adults and chironomid larvae, and few secondary prey in August. This seasonal shift in taxonomic composition is the basis for the seasonal decline in dietary diversity (Fig. 2).

ANCOVA was used to examine further the consumption of dipteran adults by brook

charr in relation to season, habitat, and heterospecific density; interactions among these factors were considered also. This analysis revealed a strong interaction between season and salmon density (Table 6). Consumption of dipteran adults by brook charr generally was less than 20 % in June and July and showed little response to salmon density, but in August, dipteran consumption by brook charr increased markedly with salmon density, from less than 20 % in sections with low salmon density to approximately 60 % in sections with high salmon density (Fig. 6). One section appeared to be an outlier, with high salmon density but low consumption of dipteran adults in August (Fig. 6). When this section was excluded from the analysis, the probability value for the interaction between season and salmon density declined from 0.018 to 0.0002. No effect of habitat was detected.

The CCA ordination for Atlantic salmon (Fig. 7) shows that dietary variation along axis 1 is related primarily to seasonal change and to variation in density of brook charr; the common prey contributing most to variation along this axis are ephemeropteran larvae (the most abundant prey in Atantic salmon diet: consumption increased seasonally and declined with increasing density of brook charr) and simuliid larvae (> 5 % abundance: consumption was highest in early summer and in sections with high densities of brook charr). The second axis is mostly associated with a contrast between pools and riffles; many prey with low abundance (< 5 %), particularly those of terrestrial origin, are better represented in pools than in riffles (also see Fig. 1); presumably this explains the differences in dietary diversity between the two habitats (Fig. 2).

Both ANCOVA approaches detected significant main effects of season and brook

charr density; neither approach detected interactions among season, habitat, and brook charr densities (Fig. 8; Table 7). Similar to brook charr, consumption of the most abundant prey changed markedly with increase in heterospecific density (Fig. 8). No effect of habitat was detected.

Discussion

Dietary diversity, overlap, and composition of brook charr and Atlantic salmon were strongly influenced by seasonal variation. For both species, densities of heterospecifics affected overall taxonomic composition of diet as well as consumption of the most abundant prey item. Consumption by brook charr of dipteran adults, its most abundant prey, was markedly influenced by an interaction between season and salmon density. No other interactive effects were detected on consumption of the main prey item for either species.

Atlantic salmon had a narrower diet in riffles than in pools. Furthermore, salmon diet was narrower in riffles than diet of brook charr in either habitat. Dietary displacement by the subordinate species in its least preferred habitat may explain lower dietary diversity of Atlantic salmon in riffles. Juvenile Atlantic salmon prefer riffles to pools, and they are better competitors than brook charr in riffles (Gibson et al. 1993; Rodríguez 1995). In pools however, larger body size and schooling behaviour seems to favour charr over salmon (Gibson 1981; Rodríguez 1995). Salmon in pools may thus broaden their diet to compensate for lower availability of preferred prey by eating a variety of less preferred taxa of terrestrial prey in small numbers.

Dietary diversity of brook charr was significantly lower in August than in June and July, mostly as a result of increased consumption of dipteran adults. Lowest dietary diversity by brook charr occurred at the same time dietary overlap between brook charr and Atlantic salmon was lowest, in August. The magnitude of dietary overlap may vary temporally due to fluctuation in resources (Schoener 1986; DuBowy 1988; Holbrook and Schmitt 1989). In periods of high food abundance, interspecific competition is likely to be minimized, but when food is scarce, interspecific competition should induce species specialization in diet (Putman 1994).

Dietary composition of brook charr and Atlantic salmon was influenced by seasonal change and abundance of heterospecifics. Seasonal variation in diet of stream-dwelling salmonids occurs frequently (Lynott et al. 1995; Bridcut and Giller 1993; Allan 1981). Because they are opportunistic predators feeding predominantly on drifting organisms (McNicol et al. 1985; Young et al. 1997), salmonids modify their diet in response to variation in abundance of drifting invertebrates over the summer (Allan 1981; Gibson et al. 1984).

Abundance of heterospecifics influenced dietary composition of brook charr and Atlantic salmon. The influence of salmon density on consumption of dipteran adults by brook charr changed seasonally. Interspecific competition seems to drive brook charr to rely on allochthonous food sources, a typical shift for salmonids when aquatic invertebrates become scarce (Wipfli 1997); this shift towards allochtonous food sources is strongest at the end of the summer presumably because aquatic invertebrates are most scarce then (Hearn

1987; Young 1997). The dietary shift of brook charr from aquatic to terrestrial prey in response to salmon density may mitigate the impact of interactions with the behaviorally-dominant salmon (Gibson 1973, 1981) through exploitation of prey items poorly represented in Atlantic salmon diet. This dietary shift ultimately results in a reduction of dietary diversity by brook charr and sharper food partitioning in August.

Dietary shift by brook charr from aquatic to terrestrial prey may be accompanied change in microhabitat utilisation. Changes in spatial occupancy in response to heterospecifics have been documented in many fish species (Fausch and White 1981; Schmitt and Holbrook 1986; Motta et al. 1995; Nakano 1995). Differences in mobility and spatial distribution among drifting invertebrates may allow fish to efficiently partition food while remaining in the same general habitat (Ross 1986). Morphological traits may contribute to exploitation of terrestrial prey by brook charr, as their low body density compared to Atlantic salmon (Gibson et al. 1993) probably better enables them to exploit terrestrial prey drifting near the surface (Hunt 1975). Microhabitat shifts by brook charr in response to competition by Atlantic salmon may thus involve increased use of the upper zone of the water column. Brook charr also could be driven to feed near the stream-margin where current is low (LaVoie IV and Hubert 1994) as a consequence of interference by Atlantic salmon. Use of stream-margin habitats has been linked to higher consumption of terrestrial insects by brook charr (Nielsen 1992).

Although microhabitat shifts provide alternative feeding opportunities to brook charr, such shifts could negatively affect their energy budget and survival. Brook charr may

be forced to increase their mobility in the stream and travel longer distances to pursue prey items at the water surface (McLaughlin et al. 1994). They would thus incur a higher foraging cost than if they remained stationary near the substratum and waited passively for drifting food (Pucket and Dill 1985). Further, higher mobility and increased proximity to the water surface can facilitate detection of brook charr by terrestrial predators (Martel and Dill 1995).

Consumption by Atlantic salmon of ephemeropteran larvae, the most abundant prey in the salmon's diet, declined seasonally and with increases in charr density. This result may arise from seasonal decline in availability of ephemeropteran larvae coupled with exploitative interspecific competition for this item which is very abundant in the diet of both species.

In addition to seasonal changes often analyzed in studies of fish diet, the results illustrate the advantages of examining the effects heterospecifics and habitat, as well as the potential interactions between these factors.

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Table 1. Physical characteristics and population densities of fish (numbers per 100 m^2), by stream and habitat type (Means ± SD). Sample sizes are provided also.

	Chandler Creek	North Gunn Creek	South Gunn Creek	Pools	Riffles
Physical characteristics					
Mean depth (cm)	23.7 (8.6)	15.4 (3.0)	28.4 (14.3)	29.3 (11.3)	16.0 (3.4)
Maximum depth (cm)	53.9 (22.9)	41.3 (18.0)	59.5 (19.6)	68.9 (15.3)	33.7 (7.4)
Stream width (m)	6.3 (2.2)	4.1 (1.4)	7.0 (2.3)	5.9 (2.2)	5.8 (2.4)
Canopy opening (degrees)	81.1 (15.8)	95.3 (20.2)	130.8 (26.5)	101.4 (25.5)	97.3 (32.7)
Current velocity ($m\ s^{-1}$)	0.25 (0.21)	0.29 (0.16)	0.17 (0.12)	0.13 (0.11)	0.36 (0.16)
Discharge ($m^3\ s^{-1}$)	0.33 (0.19)	0.13 (0.06)	0.34 (0.17)	0.24 (0.17)	0.32 (0.19)

Table 1 (continued).

Population density					
Brook charr	28.3 (13.6)	107.3 (64.9)	67.2 (49.4)	104.3 (66.4)	52.3 (36.1)
Atlantic salmon	34.2 (15.0)	0.0 (0.0)	27.1 (34.5)	9.0 (14.3)	24.1 (35.6)
Brook charr					
Sections	4	14	14	17	15
Individuals per section	5.8 (1.3)	12.0 (4.0)	12.2 (4.0)	11.1 (4.6)	11.6 (4.0)
Atlantic salmon					
Sections	12	0	10	8	14
Individuals per section	6.6 (1.6)	0.0 (0.0)	5.8 (2.9)	5.6 (1.8)	6.6 (2.5)

Table 2. Prey items found in brook charr and Atlantic salmon stomachs, with corresponding identification code (taxonomic classification follows Thorp and Covich 1991).

Taxonomic group	Code
Aquatic prey	
Acari	ACA
Branchiopoda and Copepoda	CRU
Diptera	
Chironomidae larvae	CHL
Simuliidae larvae	SIL
Other Diptera larvae	DIL
Ephemeroptera larvae	EPL
Gastropoda	GAS
Imagines	IMA
Ostracoda	OST
Other larvae	OTL
Plecoptera larvae	PLL
Pupae (mostly Diptera)	PUP
Trichoptera larvae caseless	TRL
Trichoptera larvae cased	TRC

Table 2 (continued).

Terrestrial prey	
Annelida	ANN
Araneidae	ARA
Collembola	CLL
Diptera	DIA
Ephemeroptera	EPA
Hemiptera	HEM
Homoptera	HOM
Hymenoptera	HYA
Trichoptera	TRA
Other terrestrial prey	OTA
Plecoptera	PLA
Vertebrates (Fish and Anurans)	VER

Table 3. ANCOVA examining the effects of season, habitat, and population densities on dietary diversity (Simpson's index, 1/D) of brook charr and Atlantic salmon.

Effect	df	F-ratio	p
Brook charr (n = 32 sections)			
Season	2	8.60	0.002
Habitat	1	0.12	0.73
Season x Habitat	2	0.69	0.51
Charr density	1	0.16	0.69
Salmon density	1	0.04	0.85
Error	24		
Atlantic salmon (n = 22 sections)			
Season	2	1.66	0.23
Habitat	1	11.18	0.005
Season x Habitat	2	1.37	0.27
Charr density	1	0.02	0.97
Salmon density	1	0.05	0.83
Error	14		

Table 4. ANCOVA examining the effects of season, habitat, and population densities on dietary overlap (Pianka's index) between brook charr and Atlantic salmon (n = 17 sections).

Effect	df	F-ratio	p
Season	2	8.25	0.009
Habitat	1	0.14	0.72
Season x Habitat	2	3.25	0.09
Charr density	1	1.47	0.26
Salmon density	1	0.10	0.76
Error	9		

Table 5. Results of canonical correspondence analyses for dietary composition (% numbers) of brook charr (n = 32 sections) and Atlantic salmon (n = 22 sections). Significance values for the sum of all eigenvalues (pSum), the first CCA axis (pAxis 1), and the second CCA axis (pAxis 2) were obtained by Monte Carlo resampling (1000 permutations). For brook charr: pSUM < 0.005, pAxis 1 < 0.005, pAxis 2 = 0.01; for Atlantic salmon: pSUM < 0.005, pAxis 1 = 0.01, pAxis 2 = 0.23.

	Brook charr		Atlantic salmon	
	Axis 1	Axis 2	Axis 1	Axis 2
Canonical coefficients for predictor variables				
June	0.225	0.995**	0.103**	0.470*
July	−0.224	0.774**	0.270	0.420*
August	0.000	0.000	0.000	0.000
Pools			−0.410*	0.950**
Riffles			0.000	0.000
Charr density			0.800**	−0.900
Salmon density	0.985**	0.800		
Correlations of predictor variables with CCA axes				
June	0.127	0.491**	0.439*	0.296
July	−0.171	0.277	0.050	−0.007

Table 5 (continued).

August	0.040	–0.690**	–0.512*	–0.308
Pools			–0.212	0.722**
Riffles			0.212	–0.722**
Charr density			0.310	–0.005
Salmon density	0.739**	–0.049		
Summary statistics for CCA axes				
Eigenvalue	0.177	0.089	0.207	0.102
Species - predictor correlation	0.795	0.702	0.801	0.819

* Significant at $\alpha = 0.05$

** Significant at $\alpha = 0.01$

Table 6. ANCOVA examining the effects of season, habitat, and heterospecific densities on percent dipteran adults in stomachs of brook charr (n = 32 sections).

Effect	df	F-ratio	p
Season	2	3.54	0.048
Habitat	1	0.07	0.80
Salmon density	1	5.12	0.035
Season x Habitat	2	0.23	0.80
Season x Salmon density	2	4.93	0.018
Habitat x Salmon density	1	0.14	0.71
Season x Habitat x Salmon density	2	2.09	0.15
Error	20		

Table 7. ANCOVA examining the effects of season, habitat, and heterospecific densities on percent ephemeropteran larvae in stomachs of Atlantic salmon (n = 17 sections). July samples were excluded because sample sizes for that month were too low for analysis.

Effect	df	F-ratio	p
Season	1	13.72	0.005
Habitat	1	1.31	0.28
Charr density	1	10.17	0.01
Season x Habitat	1	0.01	0.92
Season x Charr density	1	1.34	0.28
Habitat x Charr density	1	2.14	0.18
Season x Habitat x Charr density	1	0.20	0.66
Error	9		

Figure 1. Composition of brook charr and Atlantic salmon diets in pools (stippled bars) and riffles (open bars) (see Table 2 for taxon codes). Prey composition is expressed as mean percent numbers from all sections combined. Vertical lines represent one standard error.

Figure 2. Mean dietary diversity of brook charr (empty symbols) and Atlantic salmon (filled symbols) in pools (circles) and riffles (triangles), for June, July, and August. Vertical lines represent one standard error.

Figure 3. Mean dietary overlap between brook charr and Atlantic salmon in pools (circles) and riffles (squares) for June, July, and August. Vertical lines represent one standard error.

Figure 4. DCA ordination biplot representing brook charr (circles) and Atlantic salmon (triangles) samples and dietary items. Individual samples correspond to section means. Terrestrial prey are in italics; see Table 2 for taxon codes. The dashed line separates brook charr samples (left) from Atlantic salmon samples (right); all prey to the right of the line are aquatic. Eigenvalues: Axis 1 = 0.333, Axis 2 = 0.184.

Figure 5. CCA ordination biplot of brook charr dietary composition in relation to season (squares) and Atlantic salmon density (arrow). Terrestrial prey are in italics; see Table 2 for taxon codes. Small, medium, and large triangles represent prey taxa comprising < 5 %, 5 - 15 %, and > 15 % of diet by numbers.

Figure 6. Percent consumption (numbers) of dipteran adults by brook charr in pools (filled) and riffles (empty) in relation to salmon density and sampling period (June: squares; July: triangles; August: circles). Least-square regression lines are shown also. The arrow points to an apparent outlier (August).

Figure 7. CCA ordination biplot of Atlantic salmon dietary composition in relation to season (squares), habitat (squares), and brook charr density (arrow). Terrestrial prey are in italics; see Table 2 for taxon codes. Small, medium, and large triangles represent prey taxa comprising < 5 %, 5 - 15 %, and > 15 % of diet by numbers.

Figure 8. Percent consumption (numbers) of ephemeropteran larvae by Atlantic salmon in pools (filled) and riffles (empty) in relation to charr density and sampling period (June: squares; July: triangles; August: circles). Least-square regression lines are shown also.

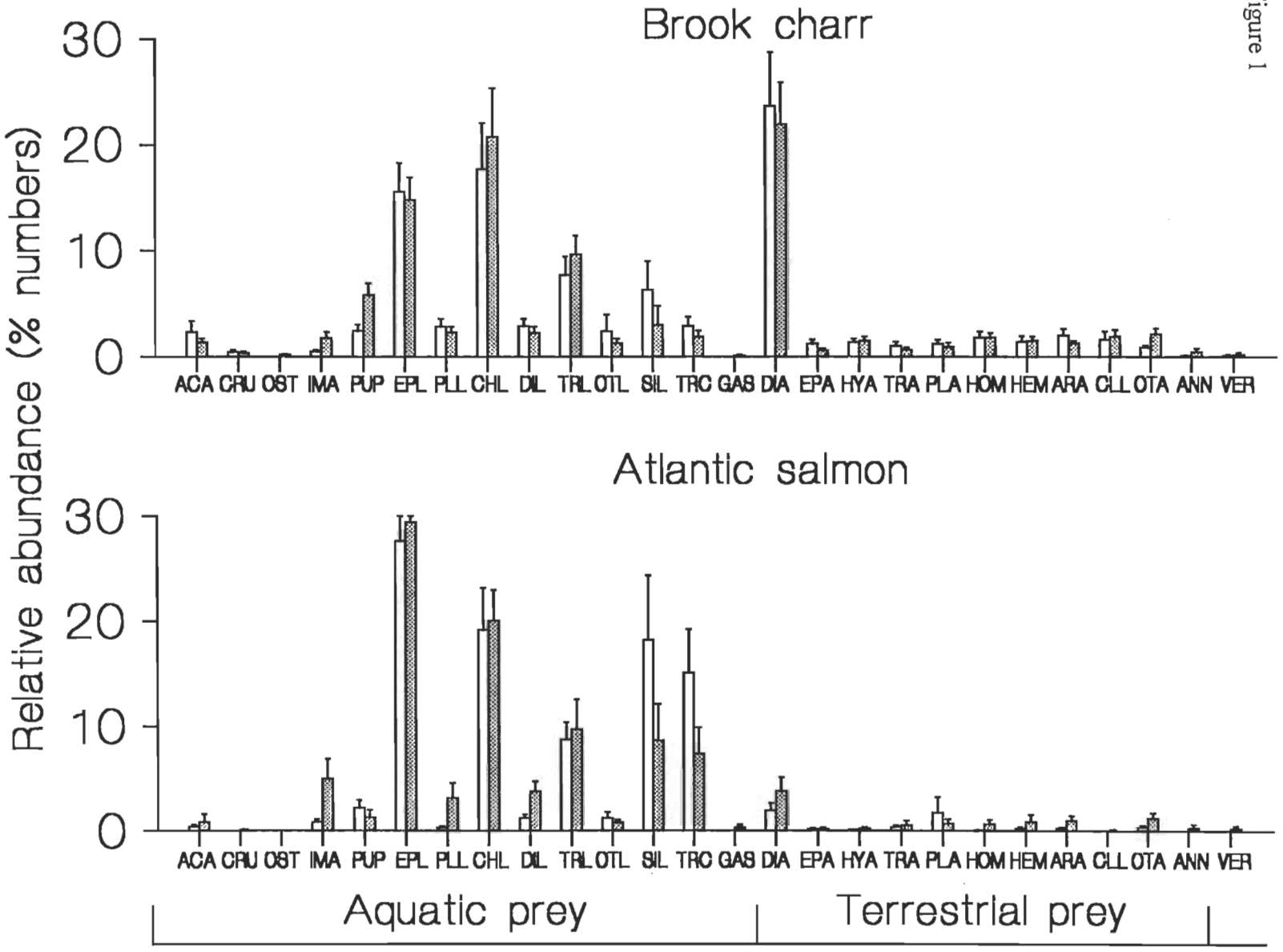

Brook charr
Atlantic salmon
Relative abundance (% numbers)
30
20
10
0
ACA CRU OST IMA PUP EPL PLL CHL DIL TRL OTL SIL TRC GAS DIA EPA HYA TRA PLA HOM HEM ARA CLL OTA ANN VER
Aquatic prey
Terrestrial prey

Figure 1

Figure 2

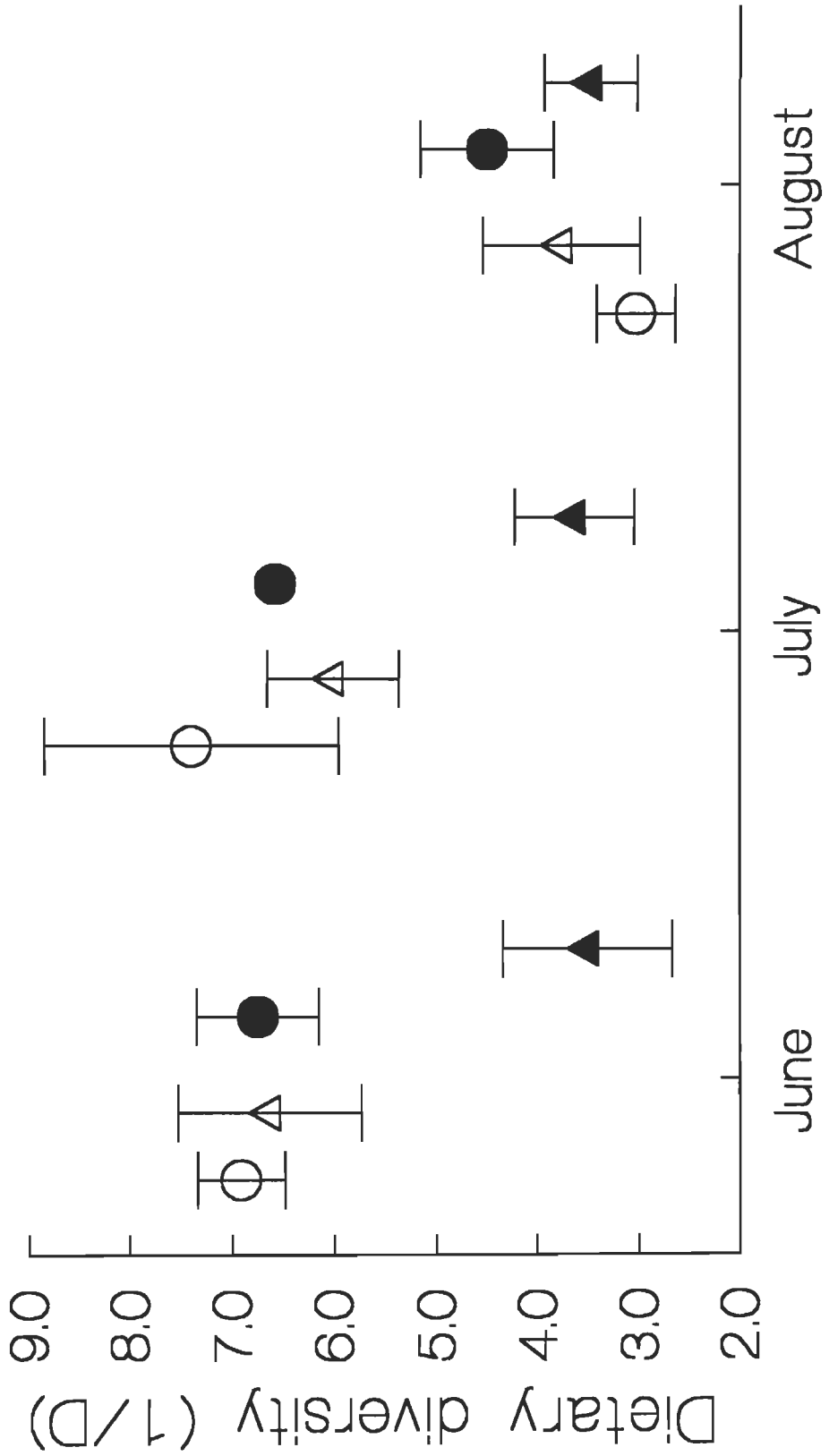


Figure 3

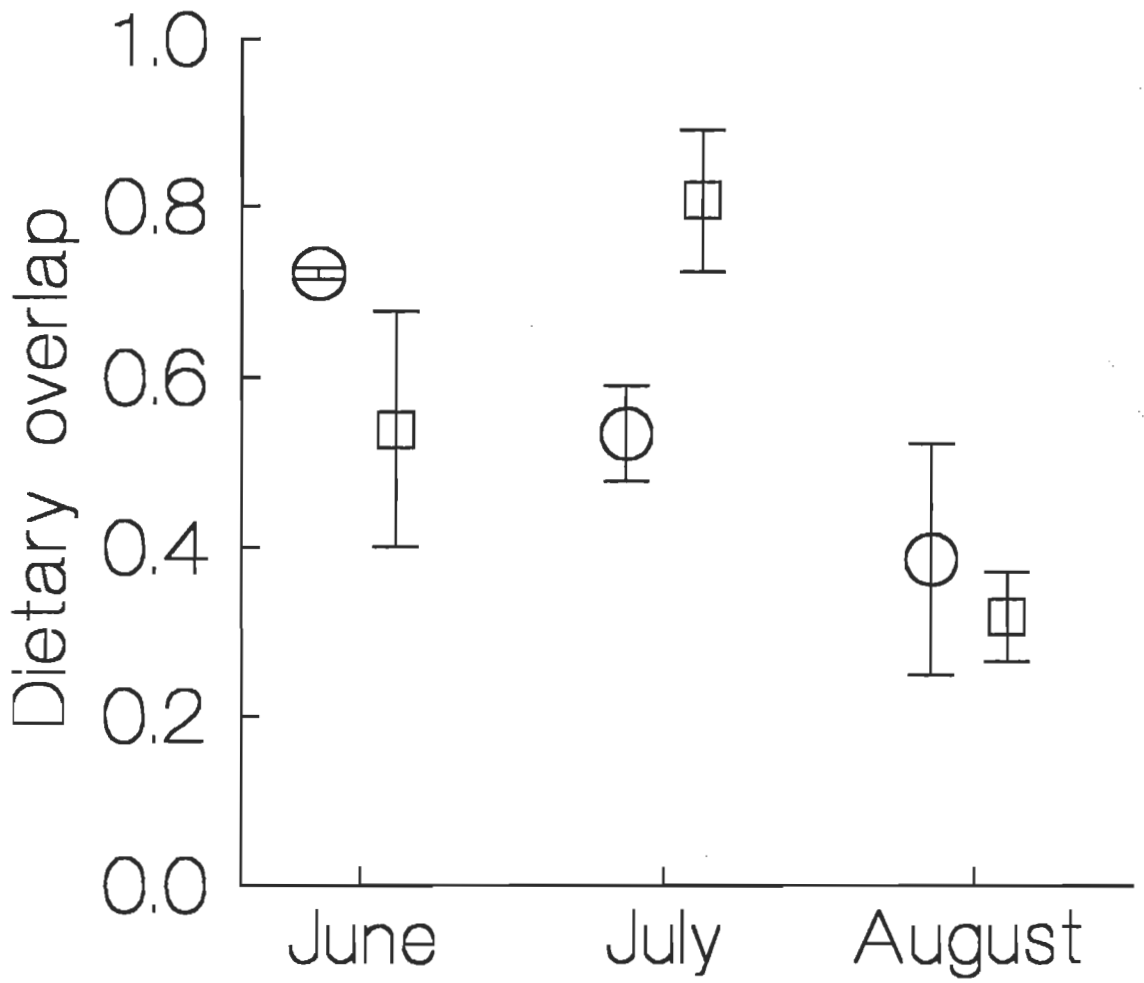


Figure 4

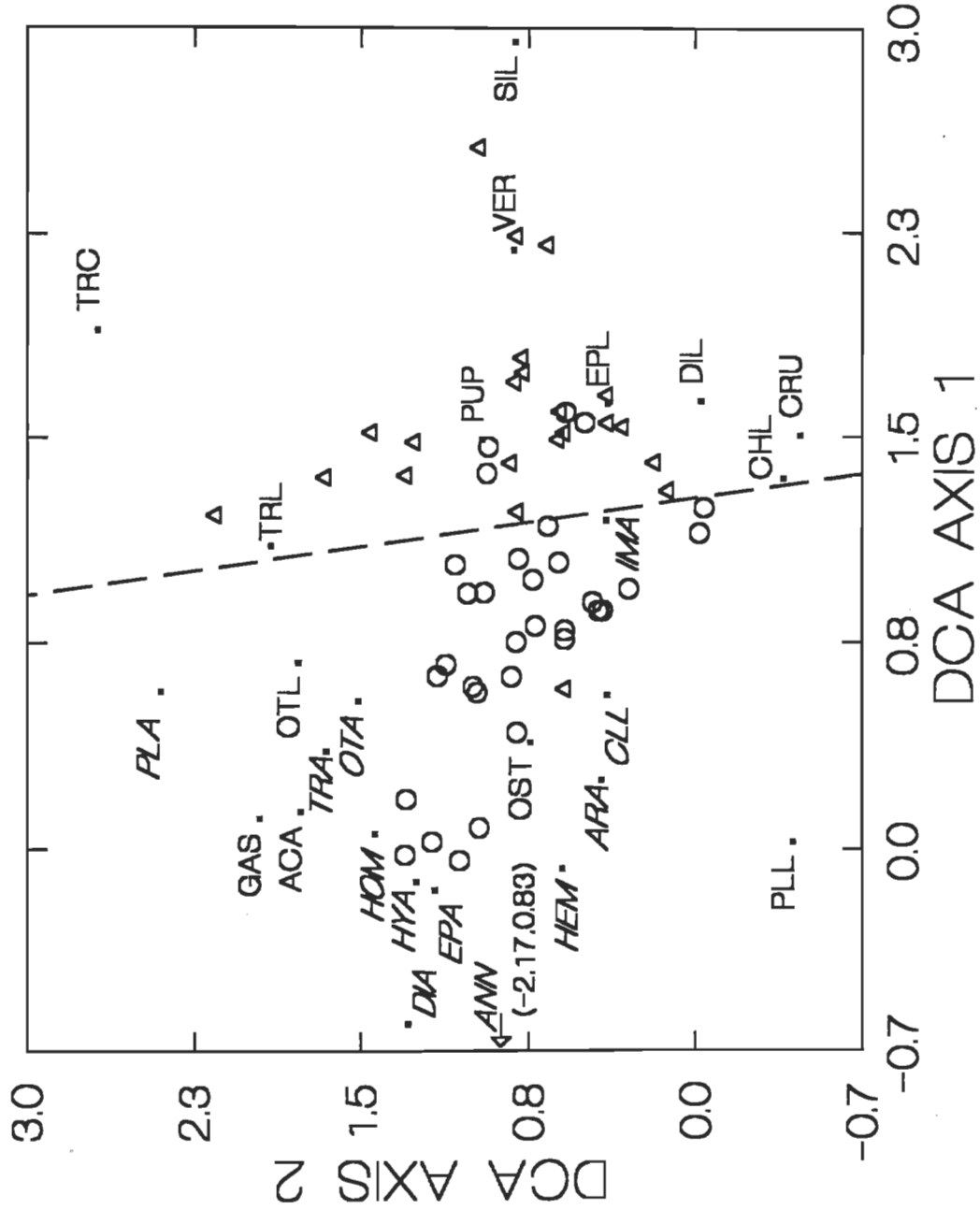

DCA AXIS 2
DCA AXIS 1
3.0
2.3
1.5
0.8
0.0
-0.7
TRC
SIL
VER
TRL
PUP
EPL
DIL
CHL
CRU
PLA
GAS
ACA
OTL
TRA
OTA
HOM
HYA
EPA
DIA
ANN
(-2.17,0.83)
OST
HEM
ARA
CLL
IMA
PLL

Figure 5

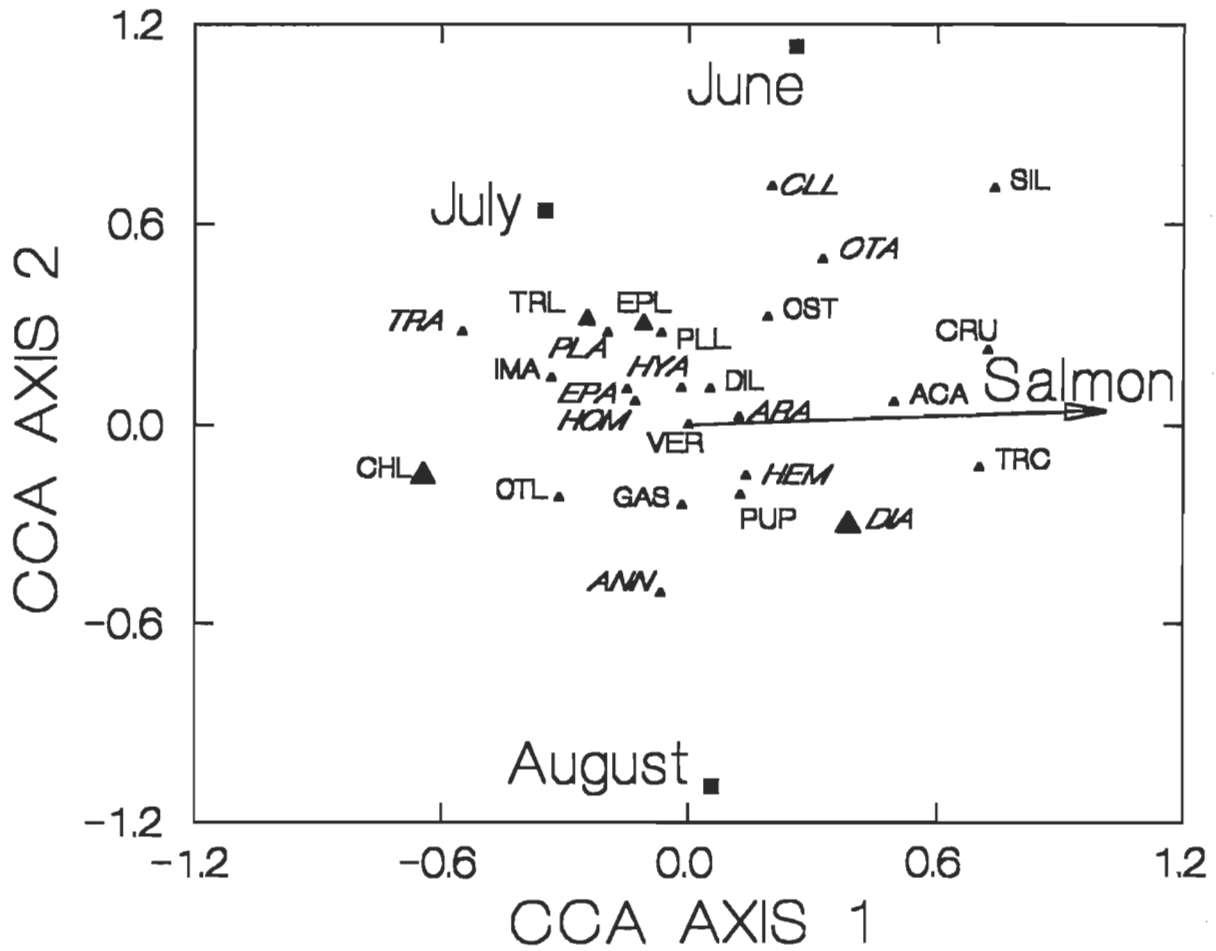

1.2
0.6
0.0
−0.6
−1.2
CCA AXIS 2
June
July
August
Salmon
CLL
SIL
OTA
TRL
EPL
OST
TRA
PLL
CRU
PLA
IMA
HYA
DIL
EPA
ACA
HOM
ARA
VER
CHL
TRC
HEM
OTL
GAS
PUP
DIA
ANN
−1.2
−0.6
0.0
0.6
1.2
CCA AXIS 1

Figure 6

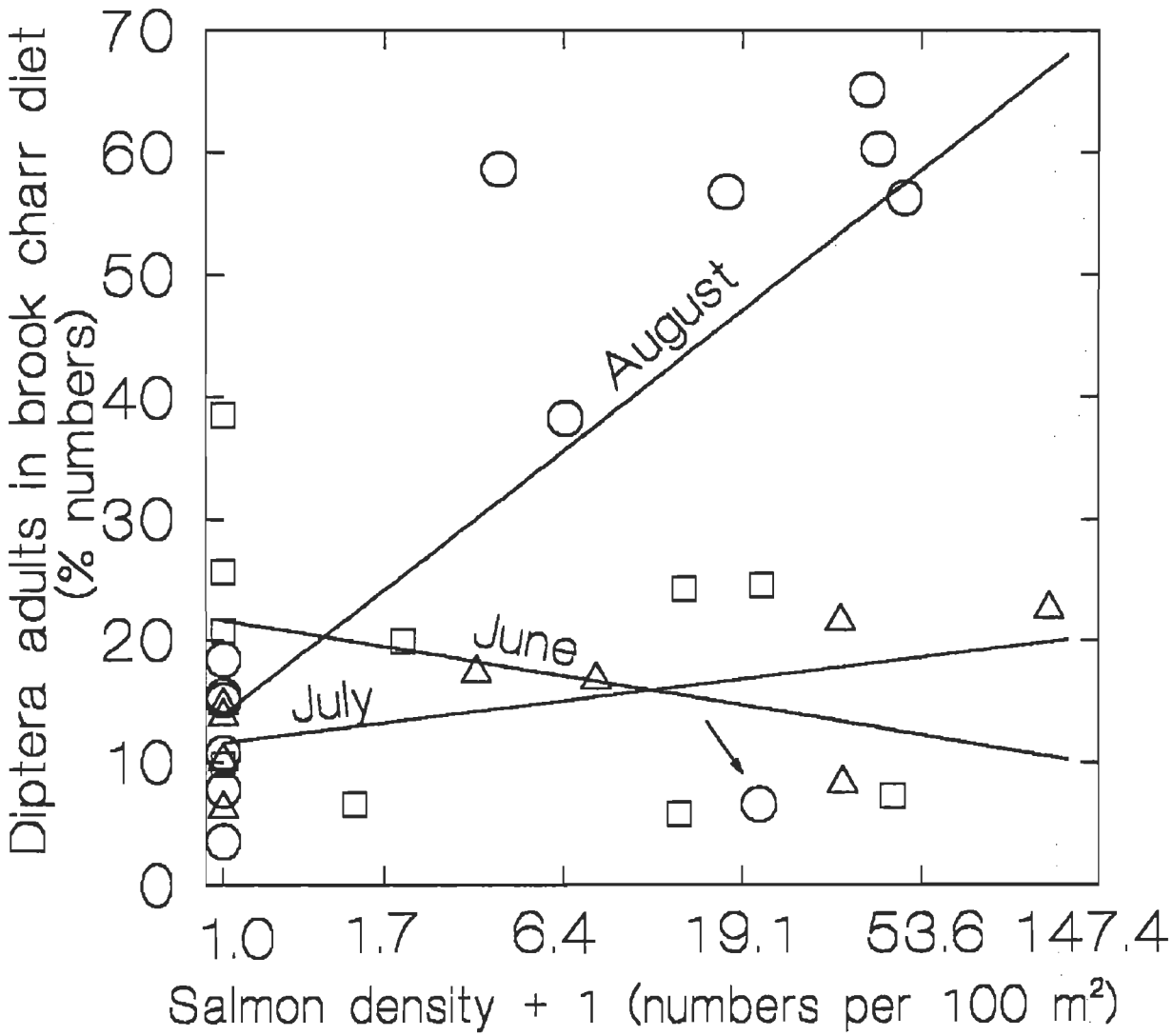

Diptera adults in brook charr diet
(% numbers)
70
60
50
40
30
20
10
0
August
June
July
1.0
1.7
6.4
19.1
53.6
147.4
Salmon density + 1 (numbers per 100 m²)

Figure 7

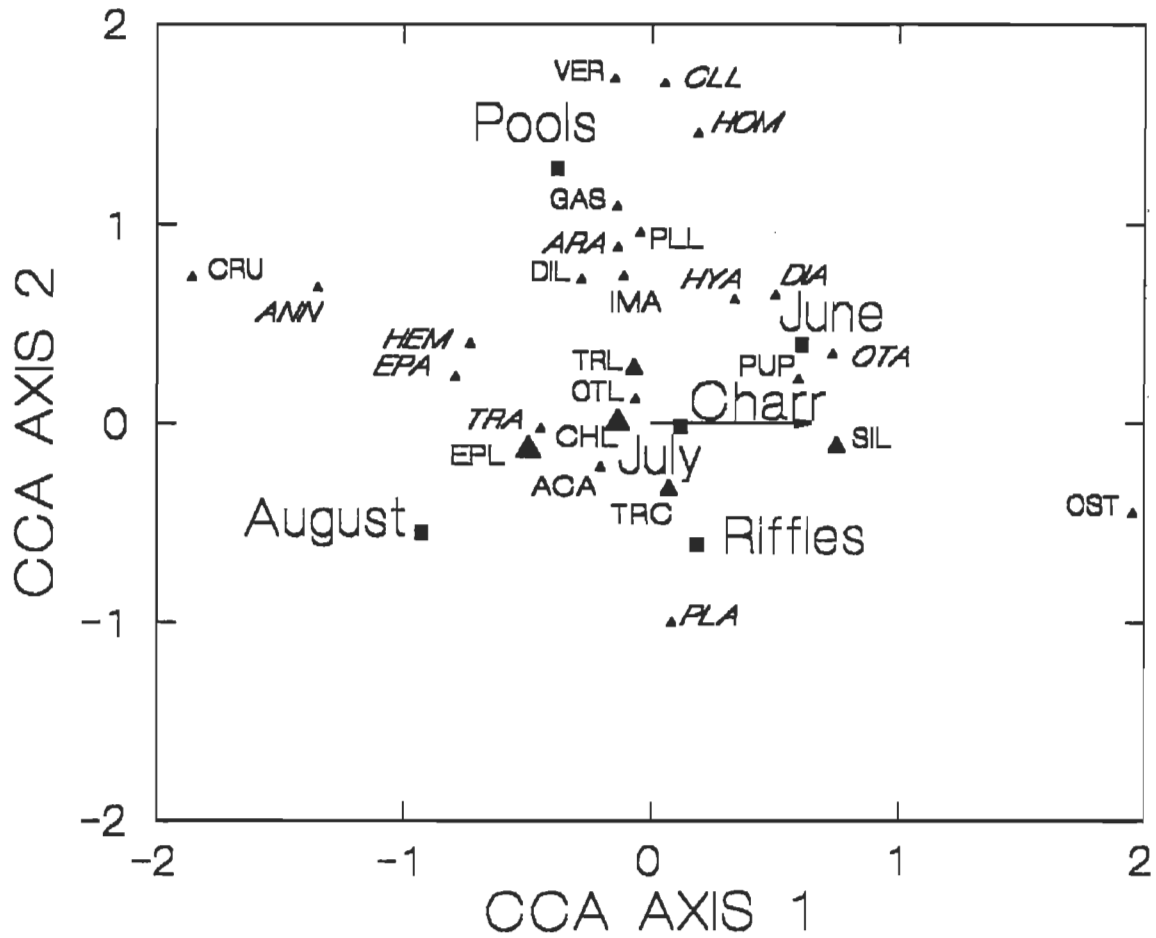
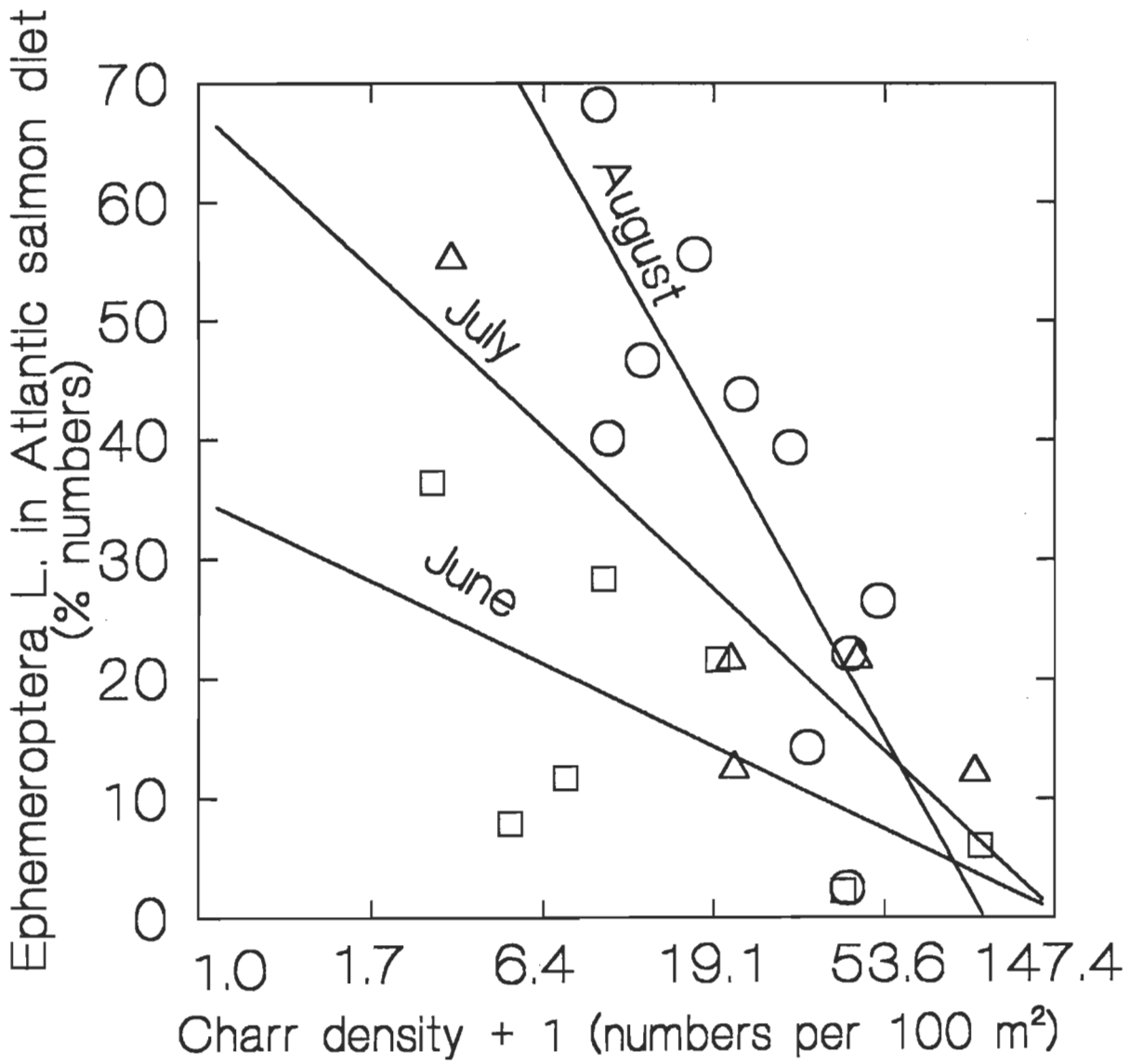

2
1
0
−1
−2
−2
−1
0
1
2
CCA AXIS 2
CCA AXIS 1
VER
CLL
Pools
HOM
GAS
ARA
PLL
CRU
DIL
HYA
DIA
ANN
IMA
June
HEM
EPA
TRL
PUP
OTA
OTL
Charr
TRA
CHL
SIL
EPL
July
ACA
TRC
OST
August
Riffles
PLA

Figure 8


Ephemeroptera L. in Atlantic salmon diet (% numbers)
70
60
50
40
30
20
10
0
August
July
June
1.0
1.7
6.4
19.1
53.6
147.4
Charr density + 1 (numbers per 100 m²)

CONCLUSIONS

Il a été démontré dans cette étude que différents aspects de la consommation de l'omble de fontaine et du saumon Atlantique en ruisseaux peuvent varier selon le temps de la journée ou la saison, l'habitat et les densités de poissons. L'omble de fontaine consommait plus de proies terrestres et moins de proies aquatiques que le saumon Atlantique. Cette différence dans l'alimentation peut être expliquée par des différences morphologiques entre les deux espèces. Le saumon possède une densité corporelle plus grande et des nageoires pectorales proportionnellement plus larges que l'omble, ce qui lui permet de se poser plus efficacement sur le substrat comparativement à l'omble qui doit utiliser une position plus élevée au-dessus du substrat.

Le taux de consommation instantané de l'omble de fontaine (mg sec de proies par g humide de poisson) atteignait un maximum en début d'après-midi (13:00), avec une faible consommation la nuit (1:00). La biomasse de dérive (mg sec de dérive m^{-2} s^{-1}) était 7,5 fois plus élevée dans la nuit (1:00) que vers midi (13:00). L'omble de fontaine se nourrit donc le jour même si la nourriture est nettement moins abondante que durant la nuit, possiblement à cause de son mode de prédation largement axé sur la vision.

Le taux de consommation de l'omble de fontaine a aussi subit des variations saisonnières avec un déclin de 41% de juin à août. Même si la biomasse moyenne de dérive au cours de la journée n'a pas déclinée de juin à août, la masse moyenne des individus dans la dérive a chutée significativement durant l'été. Le déclin saisonnier du taux de

consommation des ombles peut donc être causé par une réduction dans l'abondance d'insectes de taille profitable aux ombles.

D'autres variations saisonnières ont été notées. La diversité alimentaire de l'omble de fontaine a déclinée au mois d'août comparativement à juin et juillet, en même temps que le chevauchement alimentaire avec le saumon Atlantique déclinait. Il est possible que l'omble de fontaine compense une hausse de compétition avec le saumon à la fin de l'été par une alimentation près de la surface de l'eau. La saison et les densités de compétiteurs ont affecté la composition taxonomique du régime alimentaire de l'omble de fontaine et du saumon Atlantique; le régime alimentaire du saumon a aussi été influencé par l'habitat.

Pour l'omble et le saumon, des analyses ont été réalisées sur le type de proie le plus important de chacune des espèces. La consommation d'adultes de diptères par l'omble de fontaine était influencée par une interaction entre la saison et les densités de saumons. Durant les mois de juin et juillet, la consommation de diptères adultes variait peu en fonction des densités de saumons, mais au mois d'août, la consommation augmentait avec une hausse des densités de saumons. La consommation de larves d'éphéméroptères par le saumon Atlantique diminuait avec une hausse des densités d'ombles de fontaine. Bien que le taux de consommation journalier de l'omble de fontaine était similaire entre les fosses et les rapides, la biomasse totale d'ombles dans les fosses était 2,8 à 6,4 fois plus élevée que dans les rapides, ce qui suggère que les fosses sont plus profitables aux ombles pour l'alimentation.

Ces résultats démontrent donc qu'il est important de prendre en compte les variations saisonnières, le type d'habitat et les densités de poissons, ainsi que les interactions entre ces facteurs, lorsqu'on étudie le comportement alimentaire des poissons.

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